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Systematics of the West Indian Lizard Genus
Leiocephalus (Squamata: Iguania: Tropiduridae)

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INTRODUCTION

In the arid landscapes of Cuba, Hispaniola, and the Bahamas the swift, ground-dwelling lizard *Leiocephalus* is often recognized by the sight of its tail, which resembles a coiled watch spring. The 21 extant species compose a relict assemblage now restricted to the West Indies north of Puerto Rico (Schwartz and Thomas, 1975; Schwartz and Henderson, 1988). Two species that became extinct in the previous century and six others known only from fossils reveal that the range of this genus once included all of the major islands and banks of the West Indies, at least as far south as Martinique (Pregill et al., 1988). They are small (50 mm SVL) to large (200 mm SVL) lizards that sometimes are brightly colored, but more often drab. Some have large scales, others small. All are wary. Despite superficial dissimilarities, lizards of the genus *Leiocephalus* are a homogeneous lot.

Little is known about the natural history of *Leiocephalus* or its relationship to other neotropical squamates. A phylogeny of the species never has been proposed, although considerable detailed information is available on their geographic variation and distribution, and the taxonomy of the group is reasonably stable owing primarily to documentation of the West Indian herpetofauna by Doris Cochran and Albert Schwartz. In the late 1950's Schwartz, inspired by some of Cochran's earlier (e.g., 1941) work, initiated a series of studies on the various species

and populations of *Leiocephalus* that continued for two decades. In the end, most of the living species had been redescribed and, in some cases, affinities among them were suggested.

A second major contribution to the systematics of *Leiocephalus* was restriction of the genus to the Antillean species; since the previous century, numerous South American taxa had been included in the genus. However, Richard Etheridge (1966a), who provided the first workable diagnosis of *Leiocephalus*, recognized that evidence tying the Antillean forms with those from the South American mainland was lacking and recommended that the mainland species be consigned to *Ophryoesoides*. During the past 15 years, several more West Indian species, both living and extinct, have been named. Additionally, a handful of fossils, mostly jaw fragments, from the middle Tertiary of North America have been referred to *Leiocephalus* (Estes, 1983).

The purpose of this study is to describe the morphology of fossil and living *Leiocephalus*, to test support for the monophyly of the genus, to assess the taxonomic status of the putative North American fossils, and based on an analysis of morphological character transformations, to propose a phylogeny of the species. To facilitate these ends, a species account containing the relevant nomenclature and statements of distribution and characterization has been prepared for each species.

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McDiarmid, Elyse Beldon and Ronald Crombie, National Museum of Natural History (USNM); William Presch, California State University, Fullerton (WP). Numerous specimens in the herpetological collections of the San Diego Natural History Museum (SDSNH) also were examined.

Special thanks are extended to Donald Buden for donating a fine series of *Leiocephalus loxogrammus* that he collected on Rum Cay, Bahamas, to Uno Svensson for information on the Leiden specimen of *Leiocephalus herminieri*; and to William Presch for technical assistance with HENNIG86.

During various excursions to the West Indies, my collecting and study of *Leiocephalus* were enhanced immeasurably by the expertise and good company of Ronald Crombie, Linda Gordon, Helen James, and Storrs Olson of the National Museum of Natural History, David

Steadman of the New York State Museum, and Richard Thomas of the University of Puerto Rico. Without their participation and keen humor, along with the support and cooperation of the Smithsonian Institution, this study would have been protracted far longer than it was.

Darrel Frost and Richard Etheridge shared their ideas and insights during the course of numerous discussions on iguanian systematics, and made constructive comments on the manuscript, which was also read critically by Ronald Crombie, William Presch, Kevin de Queiroz, and Ernest Williams. Any errors in logic, observation, or style are, however, my own. Figures 5, 6, and 9 were drawn by Lynn A. Barretti.

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MATERIALS AND METHODS

Although the production of a cladogram is the logical outcome of phylogenetic analysis, explicit descriptions of character attributes should not be drafted impulsively in the desire to produce a tree. Character analysis is fundamental to phylogenetic inference despite a growing body of literature that is skewed heavily towards methodology. Occasionally we are reminded that phylogenetic algorithms are most beneficial when used to direct attention to trouble spots in the data—viz., the characters themselves (e.g., Bryant, 1989).

In selecting characters, I sought attributes that could be evaluated in two or more discrete conditions, or “states.” Hence, attention was devoted to uncovering variation in anatomical detail owing to size dependency or other causes that would swamp a character’s discreteness and render it ineffective for estimating relationships. Likewise, I know of no reasoning that would suggest that character analysis based on morphology should not yield results (Kluge, 1989). Such potential sources of information as biochemistry and karyology also might prove to be revealing, but at present, there are only isolated data of these kinds available for *Leiocephalus*.

Any discrete morphological feature was considered a potential source of phylogenetic information. There are numerous such features of the skull, the postcranial skeleton, the integument, musculature, and internal organs that have been identified in squamates (e.g., Etheridge and de Queiroz, 1988; Estes et al., 1988; Frost and Etheridge, 1989). These and others were evaluated for *Leiocephalus* and approximately 140 potential characters were examined across all ingroup taxa. Of these, 39 proved sufficiently discrete for use in phylogenetic resolution. The justification for eliminating a potential transformation was simply confrontation with continuous variation in that character (i.e., a lack of discrete states), or more commonly because meaningful variation was absent among species (i.e., all OTUs possess the same state).

After characters were identified and selected, the direction of transformation (polarity) was postulated according to the distribution of character states among hypothesized nearest relatives, the first and second outgroups (Maddison et al., 1984). When the polarity of a character could not be ascertained confidently because of ambiguous distribution of states among the

outgroups, that character was left unpolarized by scoring the ancestral condition as unknown (a “?” in the data matrix). Likewise, multiple transformations (those characters with more than two states) could not always be ordered into additive states. These were treated as “unordered” (= non-additive) so as to allow the possibility for any state to transform into another in only one step.

For ease of compilation, distributions of character states among the terminal taxa (= the species) were analyzed with Swofford's (1985, Ver. 2.4.) PAUP program, and Farris's (1988, Ver. 1.5) HENNIG86. PAUP has several options, of which I used global swapping (SWAP = GLOBAL) and multiple parsimony (MULPARS). Other utility options include HOLD, which specifies the number of trees to be held in memory at each step of tree construction. When HOLD = 1, only the

shortest, or one from the set of shortest, trees is held for the next cycle. CSPOSS and BLRANGE note character ambiguity on all but terminal stems, and maximum and minimum branch lengths, respectively. For the HENNIG86 analysis, I used the following string of commands: MHENNIG*; TPLOT; BB; TPLOT; XSTEPS; HCLM (Farris, 1988).

Characters were run without differential weighting; that is, none was assumed to have more phylogenetic meaning or content than any other. Of course, the assumption that all transformations are equally likely predictors of phylogeny is, in itself, a form of weighting that might not be true. But to do otherwise requires assumptions about development and evolution that I am not prepared to defend.

CHOICE OF TERMINAL TAXA

For the ingroup analysis, I began with the known species and subspecies of *Leiocephalus* (Schwartz and Thomas, 1976; Schwartz and Henderson, 1988) as terminal taxa. It was assumed that these taxa were valid and diagnosable, although that assumption was tested in the course of character analysis. One species of *Leiocephalus* was unavailable—the Cuban endemic *L. onaneyi* known from three specimens (Instituto de Zoología [IZ], Academia de Ciencias de Cuba; Garrido, 1973a). For all other living taxa, both wet and skeletal specimens were examined, and, in certain cases, ample series of males, females, and juveniles were available. Some species are poorly represented in collections, perhaps known only from the type series or

a single skeleton that could be prepared from a preserved series. The latter circumstance may result in the erroneous assignment of a character state to a species given that the range of variation for a character is deduced from only one, or few, individuals. A list of specimens examined is given in Appendix IV.

As to fossils, those referred to *Leiocephalus* do not provide the quantity of information comparable to that gleaned from whole specimens. Therefore, the paleospecies are not included in the primary data matrix. However, they are dealt with in a separate section following the discussion on ingroup topologies of living species and there are analyzed together with the primary data matrix.

LEIOCEPHALUS MONOPHYLY AND OUTGROUP RELATIONSHIP

In recognizing their shared attributes apart from other Iguanidae, Etheridge (1966a) informally applied the name “tropidurines” to the neotropical genera *Liolaemus*, *Ctenoblepharys*, *Phrynosaura*, *Stenocercus*, *Tapinurus*, *Plica*, *Proctotretus*, *Uracentron*, *Uranoscodon*, *Tropidurus*, and *Leiocephalus*, a group that also includes *Phymaturus*, *Strobilurus*, and *Ophryo-*

essoides. The “tropidurines” are one of eight groups of iguanian lizards the monophyly of which has been corroborated. However, “Iguanidae” in the traditional sense—all eight groups comprising a family—remains unsubstantiated as a natural taxon. There are no uniquely derived attributes that all of these eight groups share, nor is there more than suggestive evidence that would

relate one of these groups to any of the others (Estes et al., 1988; Etheridge and de Queiroz, 1988; Frost and Etheridge, 1989; Williams, 1988).

The most recent phylogenetic analysis of Iguania ("Iguanidae" + Agamidae + Chamaeleonidae) by Frost and Etheridge (1989) failed to uncover any evidence of a natural "Iguanidae." Hence, continued recognition of "Iguanidae" in the formal sense perpetuates a concept of monophyly when none exists. Frost and Etheridge sought a logically consistent recourse to this problem by proposing a revised taxonomy that formalized the eight casual groupings into family rank. The tropidurines of Etheridge (1966a), for instance, become Tropiduridae. Within Tropiduridae, a formal subfamily, Tropidurinae, replaces the casual "*Stenocercus*" group (*Stenocercus* + *Ophryoesoides* + *Proctotretus*) plus the *Tropidurus* group (*Plica*, *Uracentron*, *Uranoscodon*, *Tropidurus*, *Strobilurus*, and *Tapinurus*). In turn, Liolaeminae formalizes the *Liolaemus* group (*Liolaemus*, *Ctenoblepharys*, *Phymaturus*), which thus leaves *Leiocephalus* as a monotypic subfamily, the Leiocephalinae. The taxonomy of Frost and Etheridge (1989) is followed here. For a detailed analysis of the *Tropidurus* group, see Frost (1987) and, in part, Rodrigues (1987), and for the Liolaeminae, see Etheridge (MS).

The monophyly of tropidurids is supported by possession of an enlarged sternal fontanelle, which also occurs in phrynosomatids; however, tropidurids differ in lacking femoral pores (Etheridge, 1966a). The angular bone on the mandible is reduced in tropidurids, as it is in *Anolis* and other polychrids, and the gular fold is incomplete medially as in *Anolis* and also the phrynosomatid *Sceloporus*. Possibly, the Tropiduridae can be distinguished by a unique dentary-postdentary articulation (see below).

There is nothing compelling to suggest that *Leiocephalus* is not nested within Tropiduridae, but its relationship is arguable. When Etheridge (1966a) restricted *Leiocephalus* to the West Indian species, he concluded that it was the least easily placed tropidurine (= tropidurid) genus, but that it seemed to have affinities with the large (100+ species) South American complex *Lio-*

laemus. In more recent work, Frost (1987) and Frost and Etheridge (1989) hypothesized that *Leiocephalus* is the sister taxon of the "*Stenocercus*" + *Tropidurus* groups (Tropidurinae of Frost and Etheridge, 1989).

I employed a suite of morphological characters extracted from the literature (Etheridge and de Queiroz, 1988; Frost and Etheridge, 1989) along with my own observations to evaluate alternate outgroup relationships for *Leiocephalus*; my results corroborated the phylogeny hypothesized by Frost and Etheridge (1989) that is used here (Fig. 1): Tropidurinae as the first outgroup with Liolaeminae the second. Additional character transformations that support this phylogeny are described below.

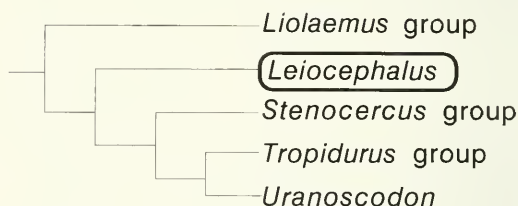


Fig. 1. Hypothesized relationships of *Leiocephalus* with other Tropiduridae based on Frost and Etheridge (1989) and this study.

1. Dentary-postdentary articulation (Tropiduridae).—The dentary-postdentary articulation of tropidurids is unique among iguanians. The articulation is formed primarily by an elongate dentary that overlaps the surangular posterior to the apex of the coronoid; the dentary and surangular often fuse with one another in this region. On the lingual side of the jaw, the antero-ventral arm of the coronoid fits up underneath the medially produced dental shelf, flush against the surangular internally. The dentary-postdentary articulation of *Anolis* is similarly constructed, but the dentary extends proportionately further back onto the surangular. In iguanids, hoplocercids, and corytophanids, the dentary scarcely overlaps the surangular and the dentary-postdentary articulation lies directly beneath the coronoid, formed as a tongue-and-groove con-

structed around an intramandibular septum that descends from the roof of Meckel's canal (Pregill, 1981). That of phrynosomatids is similar to the iguanid joint, differing in the greater posterior extension of the dentary onto the surangular. Polarities of these various articulations are difficult to assess, and to order. Each may be derived independently. For that reason I treat the tropidurid condition only as a possible synapomorphy of the family.

2. Palatal width (*Leiocephalus* + *Tropidurinae*).—In pleurodont iguanians, the transverse width of the palatal bones at the pterygopalatine suture is nearly half or more the width of the suborbital fenestra. In *Leiocephalus* and the Tropidurinae, the pterygopalatine suture is narrow, being a third or less the width of the suborbital fenestra.

3. Quadrate (*Tropidurinae*).—In *Leiocephalus*, numerous members of the "*Stenocercus*" group, and most *Liolaemus*, the lateral conch of the quadrate is broad, deep, and notched dorsally to receive the peglike, quadrate process of the squamosal. This is a basal squamate attribute (Robinson, 1967; Estes et al., 1988). By contrast, in most *Tropidurus*, *Plica*, *Uranoscodon*, *Uracentron*, *Proctotretus*, and some "*Stenocercus*" (*humeralis*, *pectinatus*, *boettgeri*, *nigromaculatus*, *praeornatus*), the lateral conch of the quadrate is shallow, nearly flat, and slightly or not at all notched dorsally.

4. Infraorbital region (*Tropidurus* group).—The palatine alone makes broad contact laterally with the maxilla so as to separate the infraorbital foramen from the lacrimal foramen in *Tropidurus* (except west of the Andes), *Plica*, *Uracentron*, *Uranoscodon*, *Strobilurus*, and *Tapinurus*. This seems to be a synapomorphy of that group. In other tropidurids (also *Sceloporus*), the lacrimal bone is produced medially from the maxillary arch to contact the palatine; thus, more of the lacrimal and less of the palatine participates in the bridge separating the infraorbital foramen from the lacrimal foramen.

5. Fifth metatarsal (*Tropidurus* group).—The primitive iguanian fifth metatarsal is planar on the lateral side. In the *Tropidurus* group the bone is convex laterally owing to the bone being

more robust overall and having a medial inclination of the distal process.

HOMOPLASY

Frost and Etheridge (1989) discussed key instances of homoplasy (with respect to *Leiocephalus*) in their cladogram of Tropiduridae. For example, the nasal process of the premaxilla is overlapped (to varying degrees) by the nasal bones in *Leiocephalus* and the Liolaeminae; the attribute is derived in these taxa, as is the possession of a coronoid labial blade. I note the following additional convergences between *Leiocephalus* and other tropidurid taxa.

Narial foramen.—The anterior alveolar foramen located on the maxillary wall of the fossa exonarina is enlarged in *Leiocephalus*, some "*Stenocercus*," *Plica*, and *Uranoscodon*. The foramen is small or absent in other tropidurids, as well as phrynosomatids and oplurids and, therefore, is considered the ancestral state.

Sternum size.—The sternum of *Leiocephalus* (except *herminieri*) and the "*Stenocercus*" group is small relative to that of other tropidurids and most iguanians. Less than half of the sternum extends posterior of the coracoids and the central fontanelle comprises half or more the surface area of the sternum.

Scapulocoracoid foramen.—The scapulocoracoid foramen, immediately dorsal to the glenoid cavity, is conspicuously enlarged in *Leiocephalus* and the "*Stenocercus*" group. In other tropidurids and phrynosomatids, the foramen is small or absent.

Number of distal tarsals.—There are two distal tarsal elements in most squamates, numbers 1–3 having been lost. *Leiocephalus* and some of the "*Stenocercus*" group ("*Ophryoessoides*" *caducus*, "*O.*" *iridescens*) have three distal tarsals, as in *Sphenodon*; the additional element is visible on the plantar surface proximal to the ends of Metatarsals 1 and 2. Possibly the element results from a secondary center of ossification in Distal Tarsal 4. With some hesitation, I have assumed that the additional element in *Leiocephalus* and *Ophryoessoides* are homologues.

LEIOCEPHALUS MONOPHYLY

Monophyly of *Leiocephalus* is supported by the derived attributes listed below. For the sake of completeness, Table 1 provides a list of common iguanian characters for which *Leiocephalus* exhibits the ancestral state (Estes et al, 1988; Etheridge and de Queiroz, 1988; Frost and Etheridge, 1989).

Table 1. Plesiomorphic states exhibited by *Leiocephalus* for common iguanian character transformations (e.g., de Queiroz, 1987; Etheridge and de Queiroz, 1988; Frost and Etheridge, 1989; Williams, 1988).

-
-
- | | |
|-----|---|
| 1. | Parietal foramen usually at frontal-parietal suture |
| 2. | Nasal process of premaxilla narrow in some |
| 3. | Lacrima present |
| 4. | Lacrima foramen small |
| 5. | Postfrontal present |
| 6. | Supratemporal position usually lateral |
| 7. | Osseous labyrinth moderately evident |
| 8. | Splenial present, straplike |
| 9. | Angular present |
| 10. | Tooth crowns tricuspid, flared |
| 11. | Seven premaxillary teeth |
| 12. | Pterygoid teeth variously present |
| 13. | Palatine teeth absent |
| 14. | Second ceratobranchials short |
| 15. | Clavicles flat with moderate lateral flange |
| 16. | Clavicular fenestra absent |
| 17. | Median process of interclavicle long |
| 18. | Posterior coracoid fenestra absent |
| 19. | Twenty-four presacral vertebrae |
| 20. | Free ribs on lumbar vertebrae |
| 21. | Caudal autonomy present |
| 22. | Nuchal endolymphatic sacs absent |
| 23. | Scale organs smooth |
| 24. | Subdigital scale structure carinate |
| 25. | Distal subdigital scales without groove |
| 26. | Middorsal scale row present, continuous |
| 27. | Interparietal scale moderate |
| 28. | Superciliary scales elongate, strongly overlapping |
| 29. | Single elongate subocular |
| 30. | Ulnar nerve superficial to limb muscle |
| 31. | Dorsal leg innervation from peroneal nerve |
| 32. | Nasal passage straight |
| 33. | Hemipenial muscles simple (Arnold, 1985) |
| 34. | Fourteen scleral ossicles |
-
-

1. Nasals enlarged.—The nasals bones of *Leiocephalus* are large, being half again or more the width of those in other tropidurids and phrynosomatids.

2. Premaxilla.—In adult *Leiocephalus*, the base of the nasal process of the premaxilla is broad and, thus, the nasal process is triangular. The shape is obtained ontogenetically from a more uniformly tapered nasal process in juveniles (see Fig. 2 and Character 2, below).

3. Septomaxilla.—The septomaxilla of *Leiocephalus* is reduced in size and inflected ventrally at its posterior margin. In other tropidurids, the septomaxilla is larger and the posterior margin is horizontal or directed dorsally. The reduced septomaxilla of *Leiocephalus* might be correlated with the primitively short nasal vestibule in these lizards (see Frost, 1987). However, the ventral inflection posteriorly is peculiar to them so far as I can ascertain.

4. Parietal roof.—The parietal roof of adult tropidurids retains a neonatal, trapezoidal outline. In *Leiocephalus*, the sides of the parietal table converge posteromedially into a "U" or a "V" such that the adult parietal roof is more triangular than trapezoidal (Fig. 3). Among tropidurids, a convergent parietal table is peculiar to *Leiocephalus* (Etheridge, 1966a). The convergent parietal table, or a modification of it, also obtains in most iguanids and in corytophanids, with the latter group further expanding the "V" into a posteriorly directed vertical blade (Lang, 1989).

5. Cervical rib morphology.—In tropidurids, the cervical ribs of the fifth and sixth vertebrae are variously expanded distally rather than proximally, as is the case in most other Iguania. In numerous *Liolaemus*, *Phymaturus* (*patagonicus*) and a few members of the "*Stenocercus*" group (*crassicaudatus*, *caducus*), the ribs are nearly twice as wide distally as they are proximally. In the *Tropidurus* group, the cervical ribs are shaped like dumbbells, being expanded proximally and distally. *Leiocephalus* is peculiar in that the cervical ribs are strongly recurved, rather than straight, and expanded in the middle. In the absence of a discernable morphocline, I would treat the transformations in shape (from the primitive, tapered condition) as separate characters—greatly

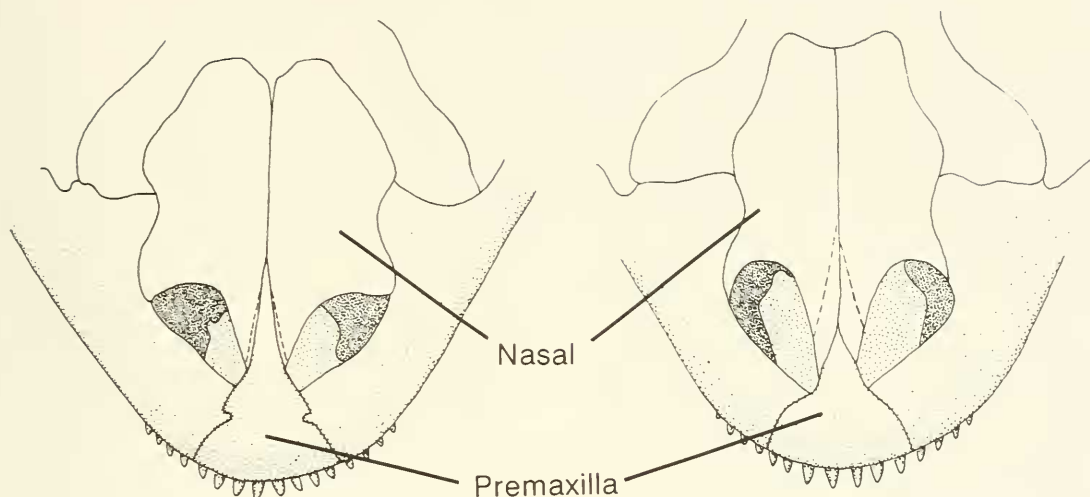


Fig. 2. Overlap of the nasal process of the premaxilla (premaxillary spine) by the nasal bones in dorsal aspect. Overlap may be minimal (left, *Leiocephalus inaguae* UMMZ 149133), leaving the nasal process exposed beyond the posterior border of the external nares or extensive (right, *L. barahonensis* SDSNH 64578) so that the process is obscured almost completely (Character 1).

expanded distally or not, and dumbbell shaped or not. The scooped, recurved condition of *Leiocephalus* is an autapomorphy of the genus.

6. Caudal vertebrae.—There are two apomorphic features of *Leiocephalus* caudal vertebrae. One is the more proximal occurrence of the first caudal vertebra bearing an autonomic fracture plane (characteristically the fifth or sixth vertebra from the sacrum). In some “*Stenocercus*” and some *Liolaemus* (also some *Sceloporus*), the first fracture plane usually occurs at the seventh vertebra, whereas in all other iguanians, it is located at the eighth or beyond. Perhaps the more anterior placement of caudal autonomy in *Leiocephalus* is correlated with their tail-curling behavior (see below). However, in another tail-waver, *Callisaurus*, the most anterior vertebra with a fracture plane is usually posterior of the eighth.

The second autapomorphy is the presence of a short, dorsally projecting spike located directly above the autonomic fracture plane (Etheridge, 1966a).

7. Interclavicle.—In most Scleroglossa, the lateral processes of the interclavicle diverge from the anterior terminus of the median process and

contact (or are overlain by) the proximal rami of the clavicles. In *Leiocephalus*, the interclavicle bears a short, median process anterior to the lateral processes—i.e., the interclavicle has an “anterior process” (Fig. 4). Thus, the lateral processes are displaced posteriorly and are free of the clavicles. Also, the posterior process of the interclavicle is broadly flared.

8. Xiphisternal rods.—In *Leiocephalus*, the xiphisternal rods continue posteriorly beyond the last (second) pair of xiphisternal ribs, whence they curve back anteriorly beneath the last pair of xiphisternal ribs (Etheridge, 1966a: Fig. 4). A parallel condition occurs in *Tapinurus*, but the recurved rods continue ventrally in association with the *M. pectoralis* (Frost, 1987).

9. Nasal and rostral scale contact.—Only *Leiocephalus* among tropidurids has the nasal scales in broad contact with the rostral scale. Apparently, *Leiocephalus* has lost the postrostral scales that separate the nasals from the rostral in other tropidurids and most other iguanians.

10. Enlarged cephalic scales.—The head scales (frontonasals, frontals, supraoculars, parietals) of *Leiocephalus* are exceptionally large relative to those of other tropidurids (Fig. 11).

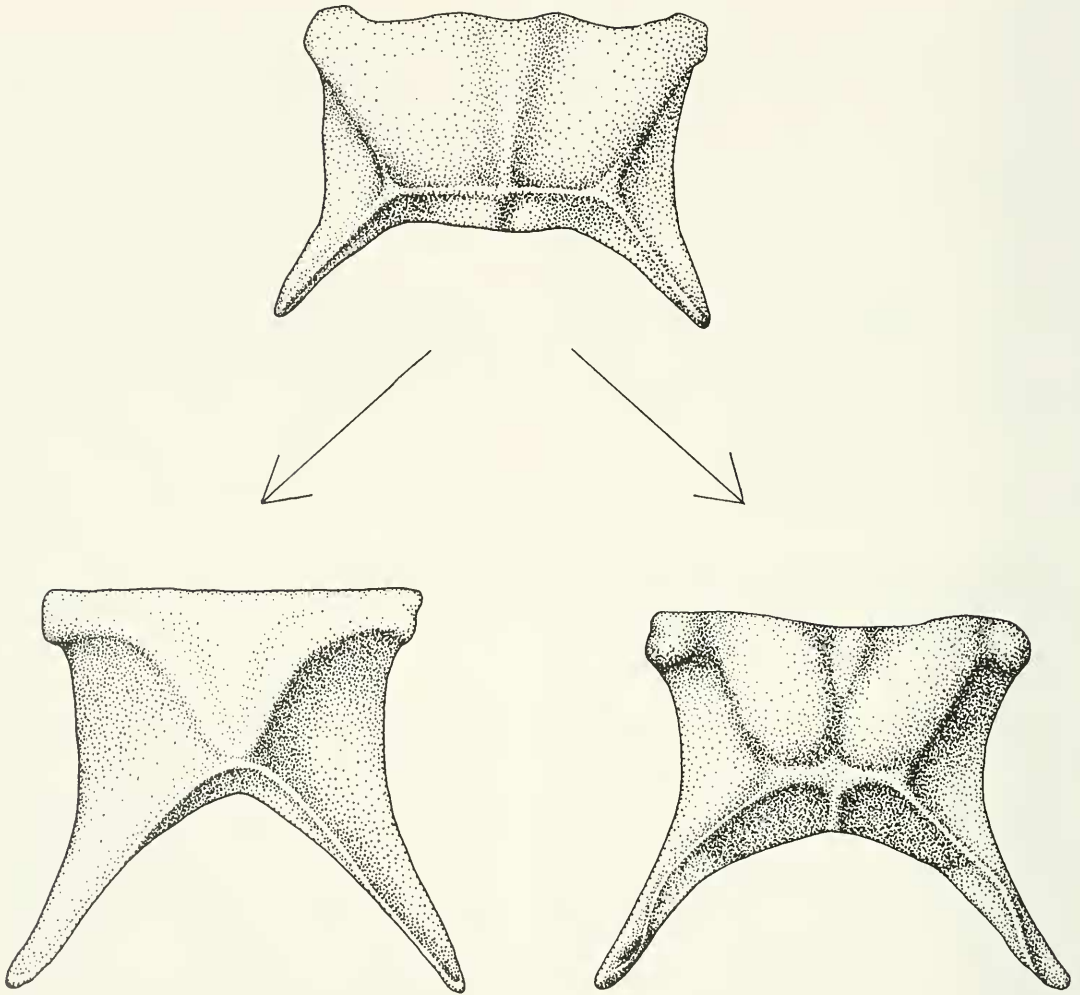


Fig. 3. The ontogenetic convergence of the parietal table in dorsal view. From a flat, juvenile condition (top) the parietal table in adults becomes either V-shaped (left) or U-shaped (right) (Character 8).

Only among some species of "*Ophryoessoides*" are supraocular scales so enlarged, but not to the extent characteristic of *Leiocephalus*.

11. Lenticular scale organs.—On the trailing edge of the paravertebral, ventral, and caudal scales of *Leiocephalus*, there are from two to five lenticular organs on either side of the median keel; the tip of the keel also bears a terminal scale organ (Etheridge, 1966a:fig. 9a). One, or occasionally two, organs are found on the paravertebral scales of "*Stenocercus*" *crassicaudatus*, some *Tropidurus* (e.g., *T. stolzmani*) and "*Stenocercus*" *apurimicus*. In "*Ophryoessoides*" *irredescens*, "*O.*" *caducus*, and species of *Liolaeminae*, there may be a terminal lenticular scale organ on the

keel. The presence of multiple scale organs on most, or all, body scales and on the tail is apparently a derived feature of *Leiocephalus*.

12. Tail curling.—As far as known, most species of *Leiocephalus* curl the tail in display, a behavioral trait unique among tropidurids. Sweeping the tail upward in a high spiral is performed by both sexes of *L. carinatus coryi* during courtship and territorial defense (Evans, 1953). Also, I have witnessed tail-curling in *L. barahonensis*, *carinatus*, *loxogrammus*, *lunatus*, *macropus*, *personatus*, *raviceps*, *schreibersi*, and *semilineatus*. Possibly, the behavior is not practiced by *pratensis* (*vide* observations by Richard Thomas published in Schwartz, 1968).

CHARACTER ANALYSIS OF *LEIOCEPHALUS*

SKULL

Numerous details of the skull were evaluated as potential transformations, but few could be characterized without insurmountable problems. Most structural details do not vary between species, but some vary intraspecifically and others are size-dependent. Much of this variation is described under the transformations enumerated (1–11) below. For reference to its general morphology, the skull of *Leiocephalus carinatus* illustrated in Figures 5 and 6, is characteristic.

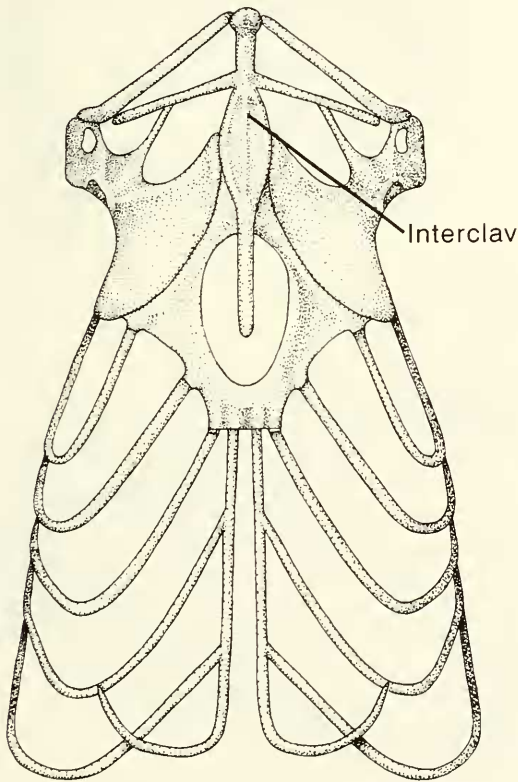


Fig. 4. The pectoral girdle of *Leiocephalus*, ventral view.

In *Leiocephalus*, snout profiles are neither strongly vaulted nor obviously depressed, as they are in some other tropidurids. Drawings of lateral views of the skull were used to measure the angle formed by the nasal process of the premaxilla and

the maxillary tooth row. The angle ranges from 42–55° as a continuous, ontogenetic and individual variable, thereby precluding any meaningful partitioning into discrete states. To this, the following can be added: the number and location of maxillary foramina vary individually; interorbital width becomes proportionately broader with increase in skull size; among species, the vomers, palatines, pterygoids, and ectopterygoids are similar to one another in shape and in articulations; pterygoid teeth are variably present within and among species; variation in the width of the interpterygoid vacuity is largely an artifact of skeletal preparation and skull size; the posterior processes of the basisphenoid vary in their encroachment onto the sphenoccipital tubercles, but variation is inconsistent within a species; other details of the basicranium are remarkably consistent from one species to the next.

I have attempted to interpret characters conservatively in order to minimize ambiguity in character-state assignment.

1. Nasal overlap of premaxilla (Fig. 2).—In *Leiocephalus* and the *Liolaeminae*, the nasal process of the premaxilla (hereafter referred to as the “premaxillary spine”) is enveloped dorsally and ventrally by the nasal bones. In all other tropidurids, the premaxillary spine overlies the anteromedial confluence of the nasals, as in many squamates. In *Liolaemus*, the nasal bones may overlap the distal end of the premaxillary spine, characteristically that portion posterior to the external nares. Within *Leiocephalus*, increasing nasal overlap accompanies ontogeny in most species, such that in adults, the nasals cover as much as two-thirds of the spine. Increasing overlap of the premaxillary spine (State 1) is characteristic of all *Leiocephalus* except for eight species in which the nasals fail to converge completely over the distal half (State 0): *greenwayi*, *herminieri*, *inaguae*, *loxogrammus*, *punctatus*, *psammotromus*, some *carinatus*, and some *hunatus*.

2. Premaxillary shape (Fig. 2).—The shape of the nasal process of the premaxilla varies with size, being nearly parallel-sided in small indi-

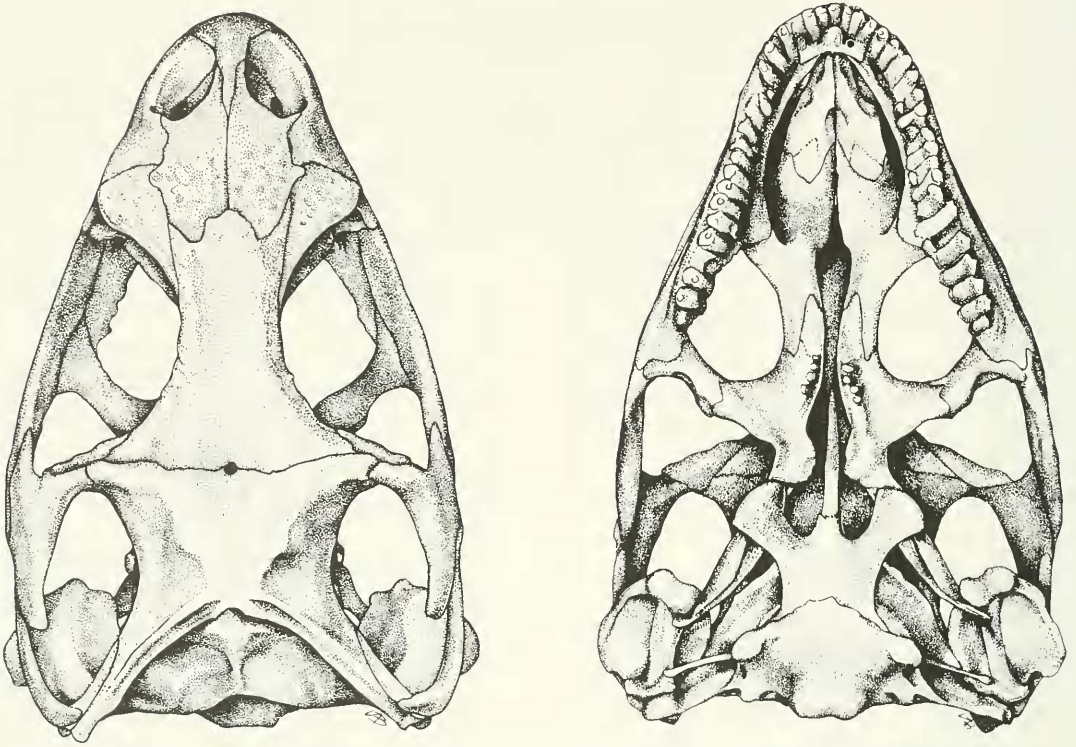


Fig. 5. The skull of *Leiocephalus carinatus varius* (USNM 217299) in dorsal and ventral views.

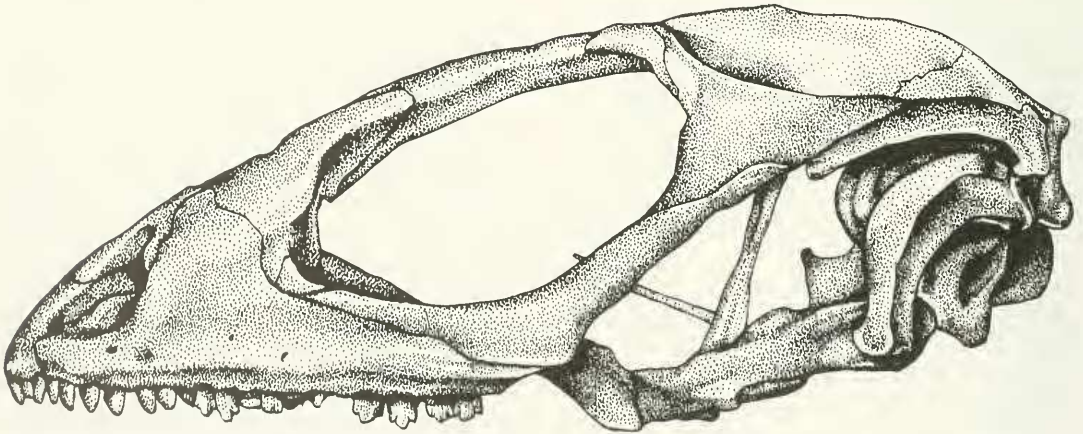


Fig. 6. The skull of *Leiocephalus carinatus varius* (USNM 217299) in lateral view.

viduals, but triangular in larger forms. However, one discrete feature is discernable. In adult *L. inaguae*, *macropus*, *punctatus*, *psammodromus*, and *schreibersi*, the base of the premaxillary spine is constricted just dorsal to the dentigerous

process (State 1). In all other species, including outgroup taxa, the sides of the premaxillary spine are parallel or evenly tapered (State 0)

3. Premaxillary spine, lateral spike (Fig. 2).—In *inaguae* and *psammodromus*, there is a

short, laterally projecting spike on either side of the premaxillary spine immediately dorsal to the basal constriction (State 1). A lateral spike is absent in other *Leiocephalus* and the outgroups (State 0).

4. Nasal-maxillary suture.—The nasal bones of *Leiocephalus* form the dorsal and lateral walls of the bony external nares. The anterolateral processes of the nasals curve and taper down the anterior side of the nasal process of the maxilla, but the extent of that overlap varies among individuals. Dorsally, on the snout, nasal articulation with the maxilla in most *Leiocephalus* is characteristic of other tropidurids—i.e., the nasal-maxillary suture arcs toward the midline of the snout as a consequence of the dorsomedial extension of the nasal process of the maxilla (State 0). In *L. himatus*, *rhutidira*, *semilineatus*, and *vinculum endomyschus*, the nasal-maxillary suture is nearly straight-sided, exhibiting minimal convergence toward the midline of the snout (State 1).

5. Nasal processes of frontal exposure (Fig. 7).—In tropidurids, the prefrontal abuts the nasal bone for half or more the length of the lateral margin of the nasal bone itself. The nasals and prefrontals contact one another and thereby obscure the nasal processes of the frontal bone (State 0). Occasionally, the nasals and prefrontals do not meet posteriorly and the nasal processes of the frontal are exposed between them (State 1). The extent of nasal-prefrontal contact may vary within species, particularly among juveniles and subadults in which reduced contact is seen more often. Nonetheless, the pattern is sufficiently consistent to characterize (Fig. 7). Reduced nasal-prefrontal contact in adults occurs in *L. greenwayi*, *herminieri*, *loxogrammus*, *macropus*, *punctatus*, *rhutidira*, *vinculum endomyschus*, some *carinatus*, and some *personatus*. Because both states occur among the “*Stenocercus*” group (*crassicaudatus*, *guentheri*, *rhodomelas*, *iridescentis*), *Plica*, *Urocenteron*, and the *Liolaeminae*, the polarity of this character is equivocal (ancestor = ?).

6. Septomaxilla.—As characters, septomaxillae are treacherous to evaluate because of their comparatively small size, entrenchment within the nasal chamber, and the fact that they are

delicate bones easily damaged in skeletal preparation. Few are preserved in series sufficient to provide confident description and comparison. The following transformation, therefore, is offered cautiously.

The septomaxilla of *Leiocephalus* is a small, saddle-shaped bone that follows the plane of the premaxillary spine proximally, and then curves ventrad toward the vomer, rather than continuing anterodorsally in the direction of the premaxillary spine. The bone is similar to that of other tropidurids in bearing a square to rectangular lateral wing with a thin, posteriorly directed process protruding freely into the nasal cavity (State 0). In *L. herminieri*, *loxogrammus*, *melanochlorus*, and *psammodromus*, the lateral wing and posterior process are reduced or absent (State 1).

7. Frontal, posterior width.—In some *Leiocephalus*, the posterior half of the frontal is unusually wide and flat, and the interorbital region is less narrow and furrowed (less concave) than in other species (State 1). A narrow frontal is primitive for tropidurids (State 0). Admittedly, “width” is subjective, and length/width ratios of adult frontals do not reveal an obvious difference from what I would consider narrow or wide frontals in *Leiocephalus*. Nonetheless, visual comparison was sufficiently compelling to score as derived the wide, flat frontal of *inaguae*, *macropus*, *melanochlorus*, *pratensis*, *psammodromus*, and *punctatus*.

8. Parietal table, convergence (Fig. 3).—All *Leiocephalus* undergo an ontogenetic vaulting of the parietal table (Etheridge, 1966a). In juveniles, the parietal table is comparatively broad and flat, not unlike that of other tropidurids as adults. With growth, the lateral faces of the parietal steepen and converge posteromedially toward one another as a raised ridge that is U-shaped in some species (State 0) and V-shaped in others (State 1). Neither seems to correlate directly with absolute size; however, the V-ridge seems to be the more derived transformation ontogenetically. Additionally, in taxa having the V-ridge, the supratemporal processes diverge from the parietal table at a more acute angle. The V-shaped ridges and associated acutely diverging supra-

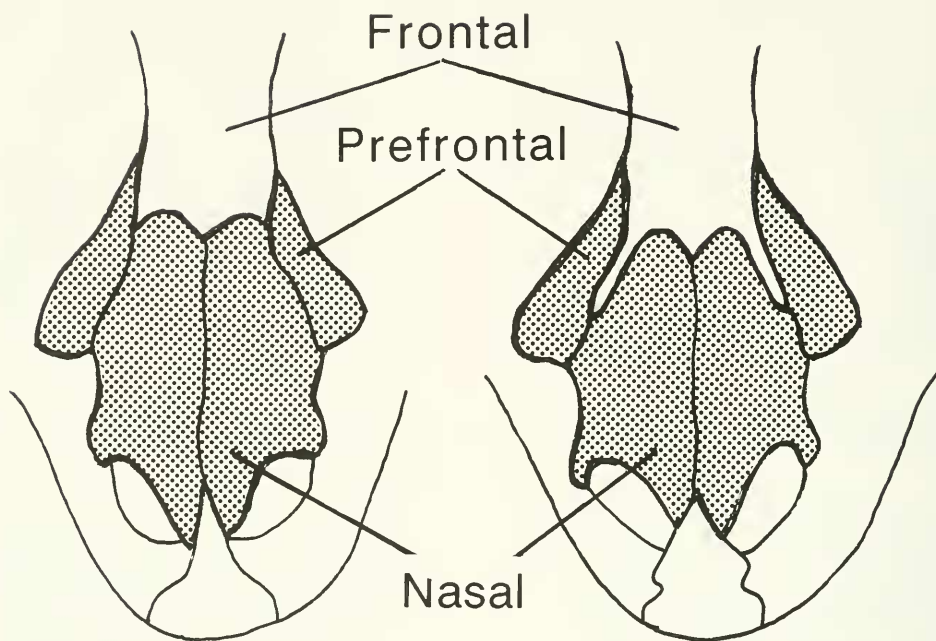


Fig. 7. Dorsal view of nasal-frontal region of the skull of *Leiocephalus*. The nasal processes of the frontal bone may be obscured by confluence of the nasals and prefrontals (left) or remain exposed (Character 5).

temporal processes characterize *L. greenwayi*, *inaguae*, *loxogrammus*, *psammodromus*, and *punctatus*.

9. Supratemporal, position.—In most *Leiocephalus*, the supratemporal bone lies on the lateral side of the supratemporal process of the parietal, as it does in tropidurids and squamates generally (State 0; Etheridge and de Queiroz, 1988; Estes et al., 1988). In *L. barahonensis*, *semilineatus*, *v. vinculum*, *psammodromus*, and some *loxogrammus* (*L. parnelli*), the supratemporal occupies a ventromedial position (State 1).

10. Squamosal (Fig. 8).—In most *Leiocephalus* and the “*Stenocercus*” and *Tropidurus* groups, the posterior end of the squamosal is expanded dorsally as a broad ridge that continues onto the anterior ramus of the squamosal. The dorsal (supratemporal) process, distinct in many iguanians, is nearly confluent with the expanded anterior ramus and is no longer evident (State 0).

In *L. psammodromus*, *melanochlorus*, and some *loxogrammus* (*L. loxogrammus*) and *macropus*, the proximal end is not expanded; thus, the anterior ramus is narrow and the supratemporal process is distinct (State 1).

11. Skull rugosities.—The dermal roofing bones (parietal, frontal, nasals) of *L. barahonensis*, some *carinatus*, *cubensis*, *greenwayi*, *herminieri*, *lunatus*, *personatus*, *raviceps*, *rhutidira*, *semilineatus*, and *stictigaster* are sculptured with an irregular pattern of prominent rugosities (State 1). In larger individuals sculpturing may include the impressions of the overlying head scales. Smooth roofing bones are characteristic of all other species and most outgroup taxa (State 0) with the exception of some individual variants of “*Stenocercus*” and “*Ophryoessoides*” (e.g., *O. aculeatus*, *O. iridescens*, *S. apurimacus*), and apparently some *Liolaemus* (Etheridge and de Queiroz, 1988).

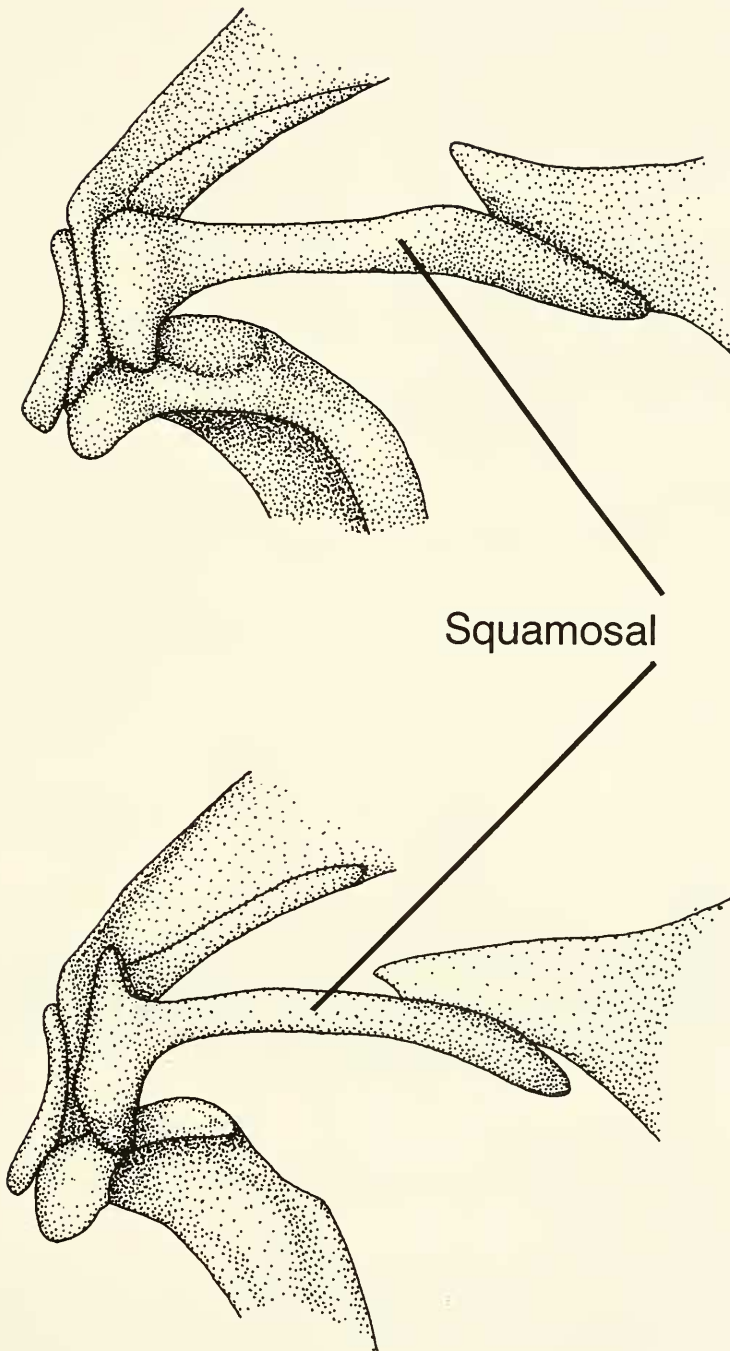


Fig. 8. The squamosal in lateral view. The bottom figure depicts the bone with a peglike supratemporal process that is characteristic of most *Leiocephalus* and numerous other iguanians. The squamosal of other *Leiocephalus* and Tropidurinae (top) lacks a well-defined supratemporal process (Character 10).

MANDIBLE

Numerous characters of the mandible have been identified in iguanian taxa and applied with varying degrees of consistency and success in phylogenetic analyses (de Queiroz, 1987; Frost, 1987; Estes et al., 1988; Etheridge and de Queiroz, 1988; Frost and Etheridge, 1989). For *Leiocephalus* (Fig. 9), I evaluated length of coronoid overlap on the anterolabial side of the dentary; length of coronoid on the anterolingual side of the dentary; shape and height of coronoid; position and/or confluence of the anterior inferior alveolar foramen and anterior mylohyoid foramen; anterior and posterior extent of splenial; position of posterior mylohyoid foramen; relationship of anterior supra-angular foramen with coronoid; number of mental foramina; shape and position of angular; shape and orientation of the retroarticular process; number of teeth, and shape of tooth crowns. None of the aforementioned occurs as characters divisible into discrete states. Two, however, could be scored—emargination of the posterior border of the dentary, and the transition from simple to tricuspid tooth crowns.

12. Dentary emargination (Fig. 10).—The posterior end of the dentary bears a dorsal surangular process and a ventral angular process, between which is a notch or emargination. Possession of an emarginate dentary may be a synapomorphy of *Leiocephalus*, because among other tropidurids it occurs only in some eastern *Tropidurus* (Darrel Frost, pers. comm.). Primatively, the back of the dentary tapers postero-dorsally so that only a surangular process exists. An emarginate dentary occurs in iguanids and corytophanids, but homology with *Leiocephalus* is doubtful because of the dissimilar construction of the dentary-postdentary articulation (see above).

Among *Leiocephalus*, the angular process is developed to varying degrees, from quite short to long, being equivalent to the surangular process in size. For this analysis, variation was collapsed into two states: (1) angular process not well developed (less than half the size of the surangular process) and therefore only modest emargination of the dentary is evident (State 0); or (2) angular process pronounced (at least half or more the size

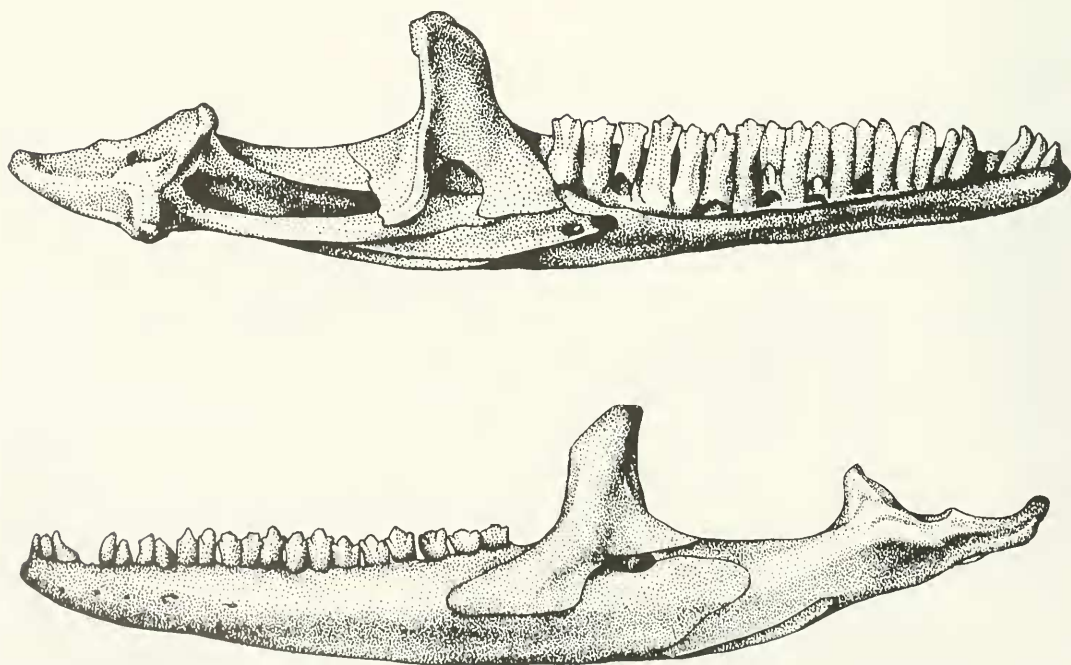


Fig. 9. Left mandible of *Leiocephalus carinatus varius* (USNM 217299) in medial (top) and lateral views.

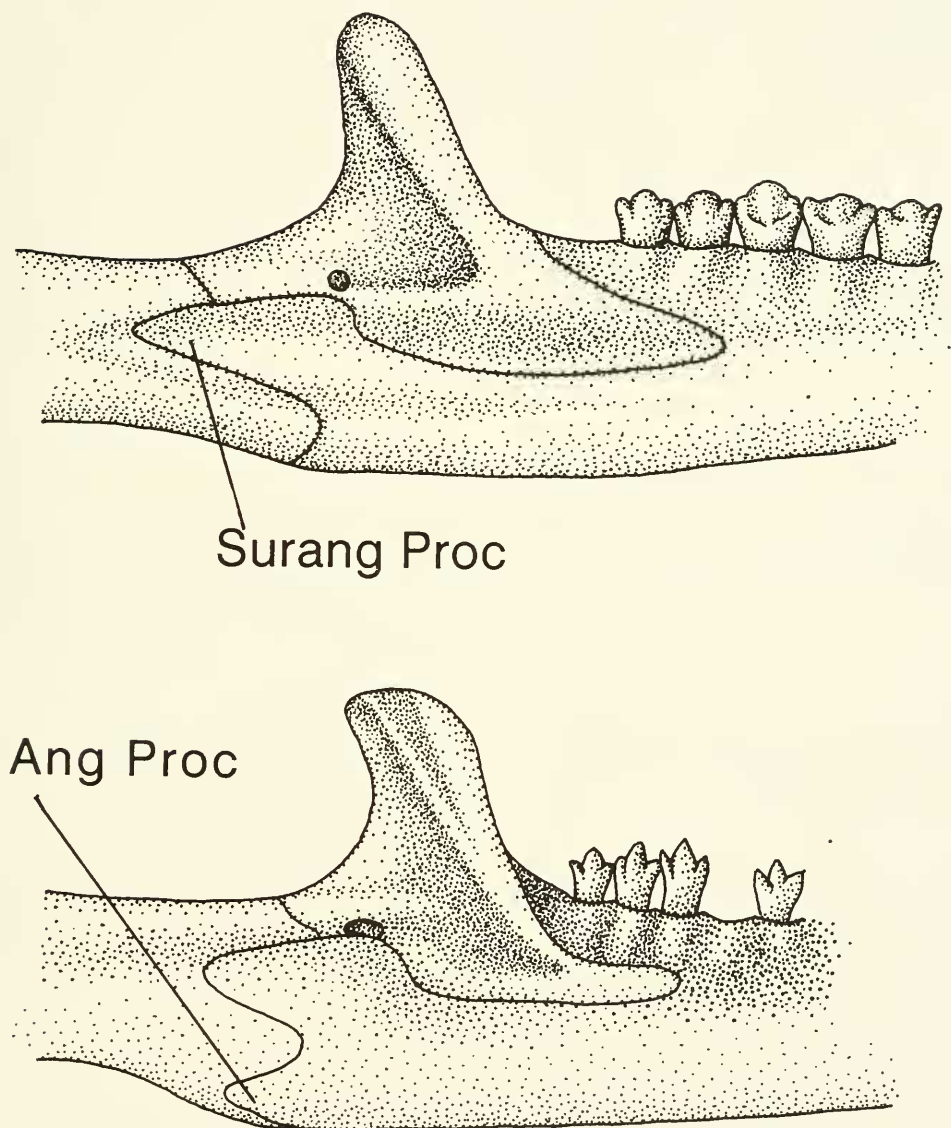


Fig. 10. Emargination of the posterior end of the dentary in some *Leiocephalus* results from a prominent angular process produced below a dorsal surangular process as in the bottom figure (*L. personatus* USNM 225041). In other species, the angular process is rudimentary and only the surangular process is evident (top, *L. psammodromus* UMMZ 149109) (Character 12).

of the surangular process), and having obvious emargination of the dentary (State 1) as is found in *L. barahonensis*, *cubensis*, *loxogrammus*,

personatus, *raviceps*, *rhutidira*, *schreibersi*, *semilineatus*, *stictigaster*, and *vinculum*.

13. Transition to tricuspid tooth crowns.—

The transition from simple, unicuspid tooth crowns to tricuspid crowns takes place anteriorly at the third or fourth tooth in *Leiocephalus rhutidira* and *L. vinculum endomychus*, and as far posteriad as the tenth or eleventh tooth in all other species except *L. greenwayi*, *inaguae*, *loxogrammus parnelli*, and *lunatus*, in which the transition occurs between the seventh to ninth teeth. Because the transition becomes more posteriad ontogenetically (i.e., as the tooth row lengthens), I evaluated this character in series of dentaries with comparable tooth row lengths (ca. 8–10 mm). A survey of outgroup species revealed that the transition to tricuspid crowns may occur on Teeth 1 or 2 (“*Stenocercus*” *roseiventris*), 5–7 (*Stenocercus apurimacus*, *Plica plica*), 7–9 (*Urocentron*, *Stenocercus boettgeri*) and 10 or 11 (“*Ophryoessoides*” *iridescent*, *Stenocercus humeralis*, *Tropidurus peruvianus*, *Uranoscodon*, and *Sceloporus occidentalis*). In some *Liolaemus*, all premaxillary and maxillary teeth are tricuspid (Richard Etheridge, pers. comm.), whereas in others, the transition from unicuspid to tricuspid crowns takes place at the fifth tooth or beyond. For this analysis, I consider only the most anterior transition (Teeth 3 or 4) in *Leiocephalus* as State 1 and all other conditions as State 0, but the character is left unpolarized.

POSTCRANIAL SKELETON

14. Vertebral neural processes.—In *Leiocephalus*, the neural spines of the midbody vertebrae are vertical and expanded distally along the longitudinal axis. This is ancestral for tropidurids (State 0). In some *L. carinatus* and *loxogrammus* (*l. parnelli*), and in *raviceps* and *schreibersi*, the spines are low, obtuse, and not distally expanded (State 1).

15. Vertebral hypapophyses.—The hypapophyses of the trunk and lumbar vertebrae (exogenous outgrowths of the centra) of tropidurids are flat, uniformly broad, and approximately half the width of the condyles of the centra (State 0). In *L. loxogrammus*, *personatus*, *raviceps*, and some *lunatus*, the hypapophyses are narrow, longitudinal ridges (State 1).

Girdles.—The pectoral girdle of *Leiocephalus* (Fig. 4) was scrutinized, but other than generic

autapomorphies (see above), no characters were discovered. Because clavicle geometry has been applied at other levels of analysis in iguanians, it is worth noting the ontogenetic change in this bone in *Leiocephalus*; the angle formed by the proximal and distal rami increases concomitant with a broadening of the bone posterolaterally. The clavicle of *L. schreibersi* is unique in being more slender distally and less acute overall than that of other species.

As with the shoulder girdle, the pelvis of *Leiocephalus* is a generalized structure and no usable characters were found.

HEAD SCALES

Most of the primary descriptions and diagnoses of extant species of *Leiocephalus* (see Species Accounts) rely exclusively on squamation of the head and body. Commonly, this includes meristic values (means and range) for prefrontals, loreals, temporals, supraoculars, supraocular semicircles, dorsal crest scales from occiput to vent, and tricarinate scales on the fourth toe. Although modal differences in scale counts are useful in differentiating species, the values are broadly overlapping and difficult or impossible to characterize and assign polarity.

The enlarged cephalic scales of *Leiocephalus* are the most distinctive feature of their squamation. Among tropidurids, the enlargement of head scales (parietals, supraoculars, prefrontals) is approached only by a few species of “*Ophryoessoides*.” The head scale patterns shared among *Leiocephalus* and described below (Characters 16 and 18) are unique.

16. Snout scales (Fig. 11).—Among *Leiocephalus*, scales of the nasal and prefrontal region (the frontonasals and prefrontals of Smith, 1946) are arranged in one of three patterns. For convenience I designate these patterns as Types I, II, and III. In the Type I pattern, there are three or, rarely, four transverse rows of subequal scales between the internasals and the anterior pair of frontals (the latter = median head scales of Schwartz, 1967a). None of these scales is enlarged, as they are in Type II and III patterns, and there are at least four scales in contact with the anterior pair of frontal scales (State 1). The Type

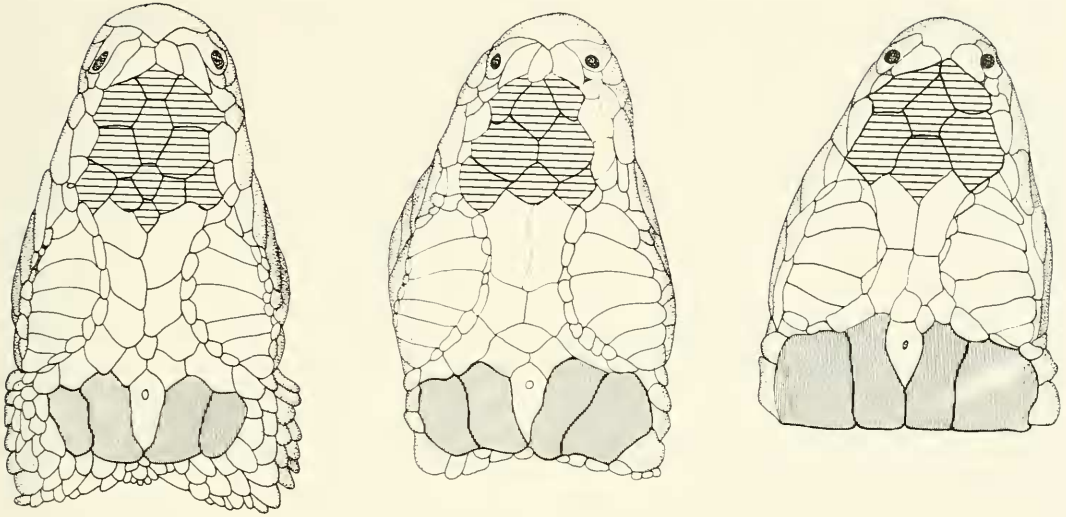


Fig. 11. Patterns of frontonasal and parietal scales. The three patterns of snout scales (horizontal hatching) in *Leiocephalus* result from a decrease in the number of frontonasals and the concomitant enlargement of those that remain. From left to right: Type I (*L. psammodromus* USNM 30385); Type II (*L. stictigaster* USNM 140466); Type III (*L. barahonensis* SDSNH 64582) (Character 16). Three patterns of parietal scale patterns (shading). From left to right: Type I, lateral parietals are smaller than medial pair; Type II, lateral parietals are equal to medial pair; Type III, lateral parietals are larger than medial pair (Character 18).

I pattern characterizes *L. eremitus*, *herminieri*, *melanochlorus*, and *psammodromus*.

The Type II pattern is a configuration of three rows of scales between the internasals and anterior frontals. The middle row may include a pair of enlarged scales (Character 17), whereas the posterior row is composed of three smaller scales in contact with the anterior pair of frontals (State 2). This pattern is characteristic of *L. carinatus*, *cubensis*, *greenwayi*, *inaguae*, *macropus*, *punctatus*, *schreibersi*, and *stictigaster*.

The Type III pattern is distinguished by two rows of scales between the internasals and the anterior pair of frontals; the posterior row is composed of three, or a single pair of, enlarged scales in direct contact with the anterior pair of frontals (State 3). The Type III pattern occurs in *L. barahonensis*, *loxogrammus*, *lunatus*, *personatus*, *pratensis*, *rhutidira*, *raviceps*, *semilineatus*, and *vinculum*.

None of these patterns is repeated among outgroup species (State 0), and although each could represent an independent derivation, the patterns seem to be related serially with the con-

dition of more numerous, smaller scales leading to one with fewer, larger scales (I \rightarrow II \rightarrow III). Nonetheless, this transformation is left unordered.

17. Frontonasal scales, enlarged pair.—Three species have a greatly enlarged median pair of frontonasal scales (State 1)—*Leiocephalus carinatus*, *greenwayi*, and *punctatus*. In all other species, these scales are not enlarged (State 0).

18. Parietal scales (Fig. 11).—There are four large parietal scales in *Leiocephalus*—a lateral pair and a median pair. Immediately posterior to the parietals there may be up to three irregular rows of small, postparietal scales occupying the nuchal fold (Character 33). As with the snout scales, there are three discernable patterns of parietal scales, which are designated as Types I, II, and III.

Overall, the parietal scales of Type I are smaller than those of either Type II or III; the most lateral parietal scales are smaller than the median pair, and there are two to four irregular rows of postparietal scales present (State 1). Type-I species include *Leiocephalus herminieri*, *inaguae*, *macropus*, *melanochlorus*, *psammodromus*, and *schreibersi*.

The Type-III pattern is extreme with respect to Type I. The most lateral parietal scales are larger than the median pair, rather than smaller, and all four scales are, overall, larger than those of Types I and II. Postparietal scales are few, more often absent (State 3). The Type III pattern characterizes *Leiocephalus barahonensis*, *carinatus*, *eremitus*, *greenwayi*, *pratensis*, *punctatus*, and *vinculum altavelensis*.

The Type-II pattern is intermediate to Types I and III; the most lateral parietal scales are subequal to, or slightly larger than, the median pair, and there is a single row (occasionally two), of postparietal scales (State 2). Type-II species are *Leiocephalus cubensis*, *loxogrammus*, *lunatus*, *personatus*, *raviceps*, *rhutidira*, *semilineatus*, *stictigaster*, and *vinculum*.

An appeal to outgroups is inconclusive with respect to the direction of transformation, and this character is left unordered. Lack of any conspicuously enlarged parietal scales is treated as the plesiomorphic condition (State 0).

19. Lateral postparietal scale, enlargement.—An apomorphy of *Leiocephalus lunatus*, *loxogrammus*, *raviceps*, and *semilineatus* is the presence of an enlarged postparietal scale on either side of the head, adjacent to each lateral parietal (State 1). These scales are not enlarged in other species or outgroups (State 0).

20. Internasal scales (Fig 11).—Most *Leiocephalus* are unique among tropidurids in having fewer than four internasals, and in having nasals that contact the rostral scale; presumably the postrostral scales have been lost in *Leiocephalus*. Only *L. herminieri* and some *psammodromus* retain four internasals. In *L. macropus* and most (70% of specimens) *pratensis* and *melanochlorus*, there are two internasal scales, whereas all other species have three. All three internasals usually contact the rostral in *L. carinatus*, *greenwayi*, *loxogrammus*, *eremitus*, and some *lunatus* (*L. arenicolor*), but in other species with three internasals, usually only two are in broad contact with the rostral, with the median internasal being smaller and posteriorly displaced. Because of considerable intraspecific variation in broad internasal contact with the rostral (i.e., 2 vs. 3 scales), I have simplified this

transformation as follows: four internasals (State 0), three internasals (State 1), or two internasals (State 2).

21. Lorilabial scales (Fig. 12).—In *Leiocephalus*, the lorilabial scale row (that row immediately dorsal to the supralabial scales) consists of four to eight scales. The two most posterior lorilabials are bordered above by an elongate subocular. In Tropidurinae and most Liolaeminae, there are three or four lorilabial scales anterior to the first lorilabial in contact with the elongate subocular. Most species of *Leiocephalus* also have four (State 0) except *L. eremitus*, *melanochlorus*, *psammodromus*, and *punctatus*. These species have five or six lorilabials anterior to the first lorilabial scale contacting the elongate subocular (State 1).

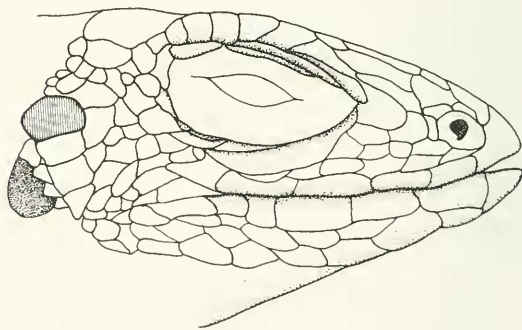


Fig. 12. Lateral head scales of *Leiocephalus barahonensis* (SDSNH 64582), showing the enlarged temporal scale (vertical hatching) anterodorsal to the ear (Character 23).

22. Cephalic scale ridges.—Many *Leiocephalus* possess multiple series of longitudinal ridges on the parietal scales, supraoculars, frontals and, in some species, most of the scales of the snout. "*Ophryoessoides*" *caducus* and *Proctotretus* have keeled head scales, but these are doubtfully homologous to the low, parallel ridges of *Leiocephalus*. Smooth head scales otherwise characterize the "*Stenocercus*" and *Tropidurus* groups and, on that basis, scale ridges in *Leiocephalus* are treated as apomorphic. The cephalic scales of *L. barahonensis*, *carinatus*, *eremitus*, *herminieri*, *inaguae*, *greenwayi*, *psammodromus*, *punctatus*, *rhutidira*, *semilineatus*, and *vinculum* are smooth

or bear indistinct ridges posteriorly (State 0). Species with ridges restricted to the parietals, supraoculars and frontals (State 1) are *L. loxogrammus*, *lunatus*, *personatus*, *pratensis*, and *schreibersi*, and those with well-defined ridges extending onto the frontonasals (the most derived condition, State 2) of this three-step transformation, are *L. cubensis*, *macropus*, *melanochlorus*, *raviceps*, and *stictigaster*.

23. Temporal scale enlarged (Fig. 12).—The temporal scales of most *Leiocephalus* are subequal, as they generally are in Tropiduridae (State 0). Dunn (1920) described the single, enlarged temporal scale anterodorsal to the ear in *L. semilineatus*, which Schwartz (1967a) also discovered in *L. barahonensis* (State 1; Fig. 12). The enlarged temporal scale is not always present in *L. semilineatus* (absent in about 25% of my sample) and it occurs with about the same frequency in *L. rhutidira*. To complicate matters, a “moderately” enlarged temporal scale occurs in some individuals of *L. lunatus*, *punctatus*, *vinculum* (except v. *vinculum*), and less occasionally, in *L. personatus*. A number of *Liolaemus* also possess an enlarged temporal scale (R. Etheridge, pers. comm.), but homology with *Leiocephalus* is unclear. Because the enlarged scale of the first three species always is located at the anterodorsal corner of the auricle, but may be more dorsal or anterior in the others, I have restricted the derived state to *L. rhutidira*, *semilineatus*, and *barahonensis*.

24. Temporal scales elongate.—Another peculiarity of temporal scalation is the presence of two or three elongate scales immediately behind the eye in *Leiocephalus loxogrammus* and *L. raviceps* (State 1). No such elongate temporals occur in other species or outgroups (State 0).

BODY SCALES

25. Neck scales, lateral.—Among *Leiocephalus*, the lateral scales of the neck are either keeled and undifferentiated with respect to the surrounding body scales (State 0), or they are smaller, and more granular with keeling reduced or absent (State 1). Neither state correlates directly with the elaboration of skin folds in *Leiocephalus* (see

below). Undifferentiated neck scales are found in *L. carinatus*, *barahonensis*, *cubensis*, *lunatus*, *personatus*, *loxogrammus*, *pratensis*, *raviceps*, *rhutidira*, *semilineatus*, *stictigaster*, and *vinculum*, whereas small lateral neck scales occur in *L. eremitus*, *greenwayi*, *herminieri*, *inaguae*, *macropus*, *melanochlorus*, *psammodromus*, *punctatus*, and *schreibersi*.

Outgroup criteria are equivocal with regard to polarity, because both differentiated and undifferentiated lateral neck scales occur among other tropidurids; hence, this character is unpolarized.

26. Trunk scales, lateral.—In *Leiocephalus*, the lateral body scales are either equal in size to (State 0), or appreciably smaller than (State 1) those scales dorsal and ventral to them, as in *L. greenwayi*, *inaguae*, *macropus*, *melanochlorus*, *psammodromus*, and *schreibersi*. Small scales co-occur with the presence of a well-developed lateral fold (Character 34) in these species, except for *L. greenwayi*. Dorsal scales that grade into smaller ones laterally also occur in some other tropidurids, for example “*Stenocercus*” and *Liolaemus*. Therefore, this character is unpolarized.

27. Middorsal crest.—A middorsal crest (from an enlarged middorsal scale row) is present in all but one species of *Leiocephalus*. However, because of continuous variation in size and shape of the scales, the crest is difficult to characterize. Only *L. pratensis* lacks a middorsal crest (State 2), whereas *L. herminieri*, *lunatus*, and *personatus* possess a crest composed of prominent, attenuate, overlapping scales (State 0). States intermediate to these extremes occur among the remaining species (State 1). Although a middorsal crest is found in most Tropidurinae, the crest may be absent, well developed, or commonly, intermediate. *Liolaeminae* lack a middorsal scale row altogether and, thus, no crest is present. This transformation series is left unordered and unpolarized.

28. Dorsal crest, scale number.—The mean number of dorsal crest scales (occiput to vent) in *Leiocephalus* varies from less than 50 in *L. melanochlorus* to more than 65 in *L. greenwayi*, *inaguae*, *psammodromus*, *raviceps*, and *schrei-*

bersi. The number of dorsal crest scales is continuously variable (nondiscrete) in Tropidurinae, ranging from few (<50) to many (>65). In *Leiocephalus*, the range of variation in the number of dorsal crest scales occurs as two unpolarized states—average number of dorsal crest scales less than 60 (State 0) or 65 or more (State 1).

29. Postanale scutcheons.—A transverse row of two, more often four, enlarged, dull white scutcheon scales lies immediately posterior to the vent in males of some species (State 1). So far as I could ascertain, such scales are absent or rare in tropidurids (State 0), but apparently do occur in some eastern *Tropidurus* (D. Frost, pers. comm.). In two taxa, *Leiocephalus rhutidira* and *vinculum endomychus*, there are as many as 12 scales arranged in three or four rows (State 2). None was observed in *L. carinatus*, *greenwayi*, *herminieri*, *melanochlorus*, or *punctatus*; occasionally, they are present in *L. psammodromus*. *Leiocephalus eremitus* is known only from the holotype female and cannot be scored.

30. Tricarinate toe scales (Fig. 13).—The tricarinate scales at the base of the first and second toes are enlarged into comblike fringes in all *Leiocephalus* (State 0) (Etheridge, 1966a). However, in some species (*L. carinatus*, *eremitus*, *pratensis*), the comb is rather poorly differentiated (State 1), whereas in *L. barahonensis*, and some *personatus* (*scalaris*) and *vinculum* (*altavelensis*), the comb is well developed and prominent (State 2). Various tropidurids also possess these enlarged tricarinate scales. I interpret their simple presence in *Leiocephalus* to be plesiomorphic, but whether the reduced comb is a primitive step, or secondarily derived, is equivocal. The transformation is unordered.

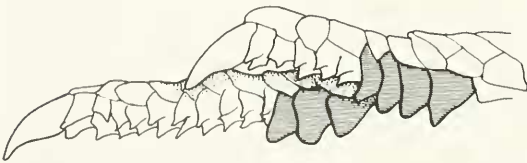


Fig. 13. Tricarinate toe scales at the base of the first and second toe enlarged into combs (*Leiocephalus barahonensis*, SDSNH 64582)(Character 30).

SKIN FOLDS

31. Antebrachial folds.—Several skin folds are common about the neck and body of iguanians. Homologies of these structures are not well established and their terminology has been applied rather casually in the past. Frost (1987) attempted to standardize the names of these folds and his recommendations are followed here. Gular and antehumeral folds are universally present in *Leiocephalus*. Topographically, the gular fold is like that of other tropidurids, but incomplete medially and oriented more obliquely (Λ) than vertically. Other neck folds are variously present among *Leiocephalus*, such that three general conditions obtain: simple—gular and short antehumeral fold only; moderate—gular, antehumeral, and oblique neck folds present; and complex—gular, antehumeral, oblique neck, longitudinal neck, and postauricular folds present. Lateral neck folds are absent, or feebly present in some “*Stenocercus*” and “*Ophryoesoides*” (e.g., *O. iridescens*, *O. caducus*, *S. festae*, *S. aculeatus*, *S. apurimicus*), whereas in other tropidurids, neck folds typically are complex. If one interprets possession of complex folds as primitive, this character is scored as a three-state transformation: complex (State 0) in *L. eremitus*, *herminieri*, *inaguae*, *macropus*, *melanochlorus*, *psammodromus*, and *schreibersi*; moderate (State 1) in *L. carinatus*, *cubensis*, *greenwayi*, *loxogrammus*, *lunatus*, *personatus*, *punctatus*, *rhutidira*, *raviceps*, *semilineatus*, *stictigaster*, and *vinculum* (*v. endomychus* only); and simple (State 2) in *L. barahonensis*, *pratensis*, and *vinculum* (except *v. endomychus*). This character is unordered.

32. Antegular scale fringe.—Evident only in some of the larger males of *Leiocephalus macropus* and *schreibersi* (and 1 specimen of *personatus scalaris*, USNM 224975) is a fold of scales on the throat that is reminiscent topographically of the antegular fold of certain tropidurids (e.g., *Plica*, *Uranoscodon*, various *Tropidurus*). These are rather unlikely homologs, however, because the structure in *L. macropus* and *schreibersi* is a convex demarcation of closely spaced scales—i.e., a fringe, rather than an in-

tegumentary fold. The absence of the scale fringe is primitive (State 0), but its presence (State 1) is applied with hesitation because of such sporadic occurrence in these species.

33. Nuchal fold.—A prominent nuchal fold is evident in all species of *Leiocephalus*. The fold, immediately posterior to the parietal scales, is a straight, transverse cleft in *L. barahonensis* and *pratensis* (State 1). The nuchal fold is moderately convex in *L. carinatus*, *cubensis*, *eremitus*, *greenwayi*, *loxogrammus*, *lunatus*, *personatus*, *punctatus*, *raviceps*, *rhutidira*, *semilineatus*, *stictigaster*, and *vinculum* (State 2), and is a strongly convex, >-shaped fold in *herminieri*, *inaguae*, *macropus*, *melanochlorus*, *psammmodromus*, and *schreibersi* (State 3). A nuchal fold is absent, or at best, poorly developed in outgroup species (State 0). I suspect that the transformation is directional in *Leiocephalus* (from straight, to moderate, to strongly convex), but that is inference, and not overly compelling; the character is unordered.

34. Lateral fold.—Some species of *Leiocephalus* possess a longitudinal fold on the side of the trunk between the fore- and hind limbs. Apparently, the presence of the structure is not a function of large body size, nor is it homologous with the dorsolateral fold of other tropidurids, which is positioned more dorsally and is often confluent with the antehumeral fold anteriorly (Frost, 1987). A lateral fold like that of *Leiocephalus* is present in some *Liolaemus*, but is otherwise absent (State 0) in tropidurids. Thus, presence of a lateral fold probably is apomorphic (State 1) for the following *Leiocephalus*: *inaguae*, *macropus*, *melanochlorus*, *psammmodromus*, *raviceps*, and *schreibersi*.

COLOR AND PATTERN

35. Ventral pattern.—As in outgroup taxa, the venter of *Leiocephalus* is dull and nearly patternless in some species, and boldly streaked, spotted or smudged in others. Patterns often vary subspecifically and only one ventral pattern could be characterized: the presence of five to seven complete transverse rows of single, dark contrasting scales in *inaguae* and *schreibersi* (State

1), and their absence elsewhere in *Leiocephalus* and outgroup species (State 0).

36. Scapular patch.—Vivid, irregularly shaped dark blotches above the forearm insertion occur in male *Leiocephalus lunatus*, and in both sexes of *L. greenwayi* and some *macropus* (e.g., *macropus macropus*). In the latter, the blotch is bisected vertically by a thin white line, and in *L. greenwayi*, there is also a dark patch above the hindlimb. Such patches seem to be apomorphic, because they are absent among outgroups, but their homology is unclear, being sex-linked in two species but not in the others. At the risk of over simplification, the simple presence of a scapular patch is scored as derived (State 1), and its absence as primitive (State 0).

37. Suprascapular blotches.—In *Leiocephalus inaguae*, *melanochlorus*, and *psammmodromus*, there are three or four dark, oblong blotches on the suprascapular region. In *L. melanochlorus*, the blotches continue onto the trunk and are vivid, whereas in *L. inaguae* and *psammmodromus*, they fade and disappear. The blotches are scored as derived in these three species (State 1). Their absence, as in most outgroup species, is primitive (State 0).

38. Facial band.—The presence of some form of a broad, longitudinal band beginning from behind the eye occurs in several species. In both *Leiocephalus cubensis* and *personatus*, the band is restricted to the side of the face as a mask. In *L. loxogrammus*, *macropus*, *pratensis*, *raviceps*, and *semilineatus*, the band continues onto the neck and shoulder, and occasionally the trunk. These markings are of dubious significance because similar features are not uncommon among outgroup species. It is equally unclear as to whether the restricted mask and band represent a single transformation. The mask and band are treated as separate states (1 and 2, respectively), with State 0 being absence of a facial band or mask. The character is unpolarized and unordered.

Throat patterns.—Among *Leiocephalus*, throat patterns vary from nearly immaculate (*semilineatus*) to faint streaks (*carinatus*), bold chevrons (*stictigaster*), distinctive spotting (*lunatus*, some *personatus*), or dull smudges

(*barahonensis*). Throat patterns often vary subspecifically (e.g. *cubensis*, *personatus*) and there is no meaningful characterization to be obtained.

OTHER CHARACTERS

Hemipenis.—The hemipenis of *Leiocephalus* is a unisulcate, weakly bilobate organ. Schwartz's (1967a:4) succinct description of the hemipenis of *L. lunatus* is typical of all species: "The sulcus is deep and prominent and is formed laterally by an extensive membranous flap from the base of the organ to near the tip. The non-sulcate surface has a series of about four flounces (which extend around the organ to near the sulcus) which rather abruptly merge into a series of about six rows of calyces. The tip of the hemipenis is smooth, weakly bifurcate and much crenulated, the sulcus extending into a cordate terminal area which includes a very weak pair of papillae. From these papillae, a raised area continues down the non-sulcate surface, expands on its proximal half, and ends at the level of the flounces on the non-sulcate surface." I found a modest amount of variation among species in the number of basal flounces, and in the degree of crenulations on the tip of the hemipenis. This insignificant variation precluded the hemipenis from further consideration.

39. Tail cross section.—Primitively in *Leioce-*

phalus, the base of the tail is terete (State 0). In *L. herminieri*, *melanochlorus*, *psammodromus*, and *inaguae*, the base of the tail is laterally compressed (State 1).

Karyology.—Karyotypes have been reported for only a few species of *Leiocephalus*; each has the presumably plesiomorphic iguanian number of 12 metacentric macrochromosomes (Gorman et al., 1967; Paul et al., 1976). There is some departure from the iguanian pattern of 24 microchromosomes, although the diploid complement of 12 + 24 occurs at least in *L. schreibersi* (Gorman et al., 1967; Paul et al., 1976:17). Unpublished data of Hall (referred to in Paul et al., 1976) mentioned "representatives of the Cuban branch of the genus to have 12 + 20 patterns," but they failed to identify which species these were. Recent work by Porter et al. (1989) disclosed a 12 + 22 diploid number for *L. carinatus*, and a 12 + 18 number for *L. raviceps*, samples of both species having been collected from the U.S. Naval base at Guantánamo Bay. In the four male *L. raviceps*, one microchromosome was much smaller than the others, suggesting an XX/XY sex chromosome system as in *Uta* and *Sceloporus*, in which the minute microchromosome is presumed to be the Y-chromosome (Porter et al., 1989). Obviously, karyological data for *Leiocephalus* are too incomplete at this time for use in phylogenetic analysis; we only know that karyotypes range from $2n = 30-36$.

TREE TOPOLOGIES FOR *LEIOCEPHALUS*

The preceding 39 transformations (summarized in Table 2 and Appendix I) were analyzed with PAUP and HENNIG86. Two minimum-length trees were found using PAUP, each having 118 steps and a Consistency Index (CI) of 0.441. The two trees differ only in alternate relationships of *Leiocephalus personatus* and *lunatus* with respect to each other and to *L. loxogrammus* plus *raviceps*. Tree no. 2 from the data output is shown in Figure 14, the support for which is discussed below. Alternate topologies (cf. Fig. 14) are also obtained using HENNIG86, although again at 118 steps (CI = 44) as in the PAUP

analysis. Four of the alternate topologies pertain to the *melanochlorus* group (see below); two describe alternate relationships for *personatus* and *lunatus*, with respect to *loxogrammus* and *raviceps* (the same two alternatives for Stem 4 in Fig. 14.), and there are three alternatives for the placement of *cremitus*. Topologies for all other terminal taxa do not vary with respect to Figure 14 except *barahonensis*.

In Figure 14 there are three clusters consisting of (1) a clade of 11 species, mostly Hispaniolan (*L. barahonensis*, *lunatus*, *personatus*, *rhutidira*, *semilineatus*, *vinculum*, *pratensis*) but also three

Table 2. Summary of character-state transformations. U = unpolarized. UO = unordered.

1. Nasal overlap of premaxillary spine complete; spine not exposed dorsally posterior of external nares.
2. Premaxillary spine constricted basally.
3. Premaxillary spine with lateral projections above constriction.
4. Nasal-maxillary suture straight-sided anterolaterally.
5. Nasal-prefrontal contact reduced.(U).
6. Lateral wing and posterior process of septomaxilla reduced or absent.
7. Frontal bone broad and flat posteriorly.
8. Parietal table narrowly constricted posteriorly. (V-shaped).
9. Supratemporal bone lies ventomedially on supratemporal process of the parietal.
10. Proximal end of squamosal not expanded, distinct dorsal process present.
11. Rugosities well developed on skull roof.
12. Surangular notch well developed; angular process one-half or more the length of the surangular process.
13. Transition to tricuspid tooth crowns (dentary) at Tooth 3 or 4.(U)
14. Neural spines low, obtuse, and not expanded distally.
15. Centra of trunk vertebrae with narrow hypapophyses.
16. Frontonasal scale pattern Type I (State 1), Type II (State 2), Type III (State 3). (UO)
17. Median pair frontonasal scales enlarged.
18. Parietal scale pattern Type I (State 1), Type II (State 2), Type III (State 3). (UO)
19. Lateral postparietal scale enlarged.
20. Internasal scales three (State 1), two (State 2).
21. Five or six lorilabial scales anterior to elongate subocular.
22. Cephalic scales with ridges present but restricted (State 1) or ridges extend onto snout (State 2).
23. Enlarged temporal scale anterodorsal to ear.
24. Two or three elongate temporal scales behind eye.
25. Lateral neck scales small; keels reduced or absent. (U)
26. Lateral trunk scales smaller than dorsal and ventral scales. (U)
27. Dorsal crest present, moderate (State 1) or crest absent (State 2). (U, UO)
28. Dorsal crest scales occiput-vent number 65 or more. (U)
29. Postanal escutcheon scales 2–4 in single row (State 1); more than 4 in multiple rows (State 2).
30. Proximal scales of first and second toes enlarged into comb (2 steps). (UO)
31. Lateral neck folds moderate (State 1) or lateral neck folds simple (State 2). (UO)
32. Antegular fringe present.
33. Nuchal fold transverse (State 1), moderately convex (State 2), or strongly convex (State 3). (UO)
34. Lateral fold present.
35. Venter with 5–7 transverse rows of pale scales.
36. Scapular patch present.
37. Suprascapular blotches present.
38. Facial mask (State 1) and band (State 2) present. (U, UO)
39. Tail laterally compressed.

Cuban (*L. cubensis*, *stictigaster*, *raviceps*), and one Bahamian (*L. loxogrammus*); (2) a clade of two western Hispaniolan species (*L. melano-chlorus*, *schreibersi*), two southern Bahamian forms (*L. inaguae*, *psammodromus*) and one Cuban (*L. macropus*); and (3) a cluster composed of two southern Bahamian species (*L. greenwayi*, *punctatus*), the extinct *L. eremitus*, and the wide-

spread *L. carinatus*. *Leiocephalus herminieri* is the sister taxon of all other species.

Stems 9 and 10.—I have some confidence that the 10 species above Stem 9 form a natural group. All taxa except *Leiocephalus lunatus* possess a dentary with an emarginate posterior border (12.1); with the exception of *L. schreibersi*, this feature is found only in this clade. Skull

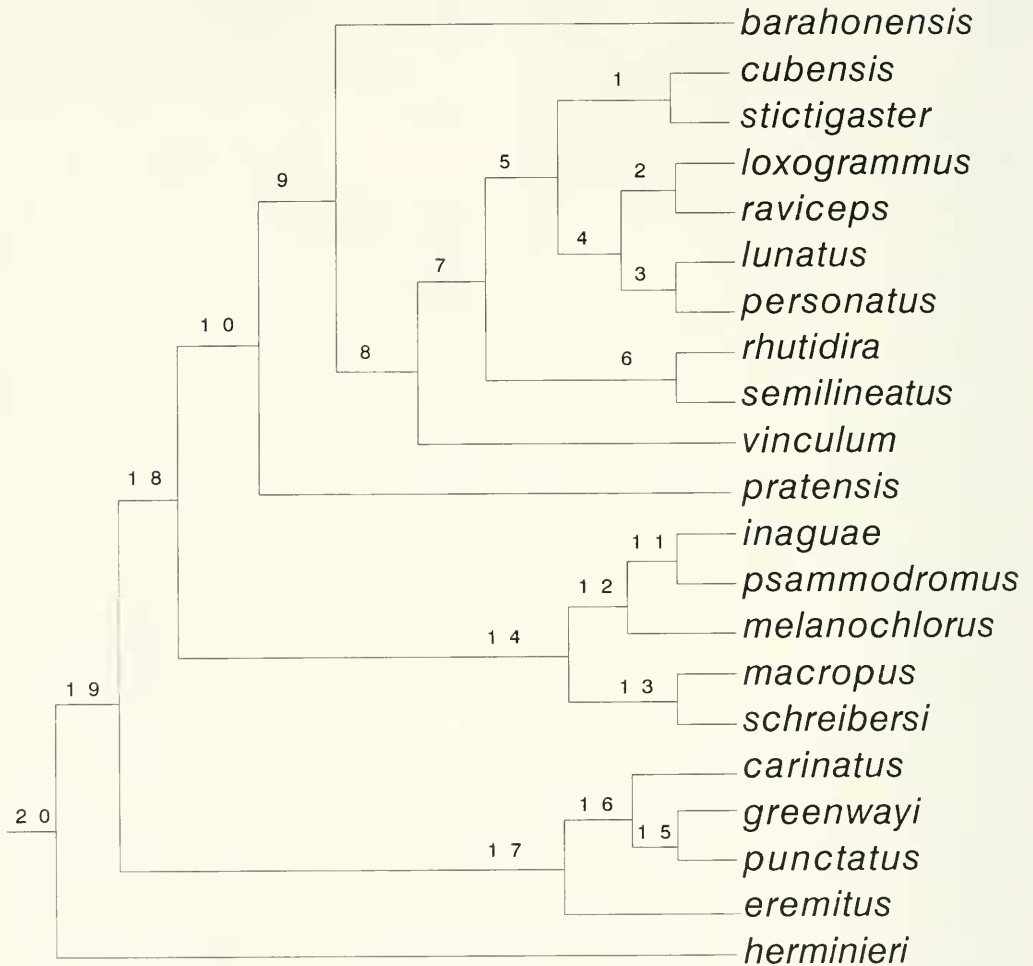


Fig. 14. Hypothesized relationships among species of *Leiocephalus* exclusive of fossil taxa based on 39 morphological characters (Appendix I) (PAUP, length = 118 steps, CI = 0.441). Support for the numbered stems is given in the text and Appendix II.

rugosities (11.1) also are acquired at this stem, but this character reverses in *L. vinculum* and *loxogrammus* and is convergent in *L. herminieri* and in *greenwayi*. Otherwise, Stem 9 is specified by three other widely homoplastic characters—a reversal to a narrow frontal (7.0), a ventromedially placed supratemporal (9.1), and smooth cephalic scales (22.0). Here, the peculiarities of *L. pratensis* are evident. This taxon is not closely related to any of the species above Stem 9 and is placed as the sister species (Stem 10) by the common possession of alternate states of four unordered,

unpolarized transformations, as follows. The presence of undifferentiated lateral neck scales (25.0) occurs in *L. carinatus*, but is otherwise unique to Stem 10. The snout scale pattern shifts from Type II (16.2) to Type III (16.3), whence it reverses at Stem 1 (*cubensis* + *stictigaster*). Antebranchial folds shift from complex (31.0) to simple (31.2) and then become moderate (31.1) at Stem 7. A straight nuchal fold (33.1) changes to a moderately convex nuchal fold (33.2) at Stem 8.

Stem 8.—The remaining nine species above *Leiocephalus pratensis* and *L. barahonensis* at

Stem 8 are uniquely united by a Type-II parietal scale pattern (18.2). There is also a shift to a moderately convex nuchal fold (33.2), which is convergent at Stem 17. As a terminal taxon, *L. vinculum* is restricted to the nominate subspecies *L. v. vinculum* from Ile de la Gonâve. On the basis of the present data and analysis, *L. vinculum altavelensis* falls out with *L. barahonensis*, whereas *L. v. endomychus* is regarded as a distinct species most closely allied with *L. rhutidira*. The character support for this scheme and a revised taxonomy are discussed in the Species Accounts.

Stems 5–7.—Stem 7 unites four pairs of species—*cubensis* + *stictigaster* and *loxogrammus* + *raviceps* in a branch with *lunatus* + *personatus* and *semilineatus* + *rhutidira* (including *endomychus*, which is not shown). The synapomorphies of this clade (Stem 7) are presence of moderately complex antebrachial folds (31.1) and a laterally placed supratemporal process (9.0); the latter represents a reversal (from Stem 9) to the plesiomorphic condition for the clade, but shows the derived condition in *L. semilineatus*. The relationship between *semilineatus* and *rhutidira* (Stem 6) is described by a straight nasal-maxillary suture (14.1; convergent in *lunatus*) and the presence of an enlarged temporal scale (23.1; found elsewhere in *barahonensis*). *Leiocephalus semilineatus* and *L. rhutidira* are linked with the three other species pairs at Stem 5 only by one widely homoplastic character—possession of restricted cephalic scale ridges (22.1). An alternate topology for Stem 7 is depicted in Figure 15 and discussed below.

Stems 2–4.—Two species pairs are united at Stem 4 (Fig. 14; *lunatus* + *personatus* and *loxogrammus* + *raviceps*) by one uniquely derived state—narrow hypapophyses on the trunk and lumbar vertebrae (15.1). The presence of a large lateral postparietal scale (19.1) also occurs at this node, but this feature is reversed (19.0) in *L. personatus* and convergent in *L. semilineatus*. There are no transformation states unique to *L. personatus* and *L. lunatus* (Stem 3); however, except for *L. herminieri*, only these two taxa possess a dorsal crest composed of attenuate, strongly overlapping scales (27.0), a character that was treated

as unordered and unpolarized. An equally parsimonious alternative links *L. lunatus* as the sister species of *loxogrammus* + *raviceps* based on their common possession of a large lateral postparietal scale (19.1). This, of course, requires the presence of attenuate, strongly overlapping dorsal crest scales (27.0) to be convergent in *L. personatus*. The evidence uniting *L. loxogrammus* and *L. raviceps* as sister taxa (Stem 2) is stronger; only these two species have elongate supratemporal scales behind the eye (24.1) and, except for *L. schreibersi*, these are the only species that possess low, obtuse neural processes (14.1). *Leiocephalus loxogrammus* and *L. raviceps* also display a facial band (38.2), but this feature is widely convergent elsewhere on the tree.

Stem 1.—Stem 1 (*cubensis* + *stictigaster*) is specified by a shift from a Type-III to a Type-II pattern of snout scales (16.2) and well-defined cephalic scale ridges that extend onto the frontonasals (16.2). Both of these transformations are homoplastic, but the sister relationship between *Leiocephalus cubensis* and *L. stictigaster* seems quite credible against the backdrop of the entire tree. This analysis actually produces a minimum stem length of 0 for *stictigaster*; however, this species is separable from *L. cubensis* by the distinctly lineate dorsum and smaller body size of *L. stictigaster*.

Stem 14.—The best supported branch on the tree is that uniting species referred to herein as the *Leiocephalus melanochlorus* group (*inaguae*, *psammodromus*, *melanochlorus*, *macropus*, *schreibersi*). Although there is only one apomorphy unique to Stem 14 (a Type-I parietal scale pattern [18.1]), three other transformations that occur at this stem are specific save for usually single occurrences of the shared state elsewhere. These taxa possess a basally constricted premaxillary spine (2.1; also *punctatus*, and reversed in *melanochlorus*), small lateral trunk scales (26.1; also in *greenwayi*), and a distinct lateral fold on the trunk (34.1; also in *raviceps*). Possession of a strongly convex nuchal fold (33.1; also in *herminieri*) is peculiar to these species as well, but as an unordered transformation, this state first appears on the ancestral stem of the tree.

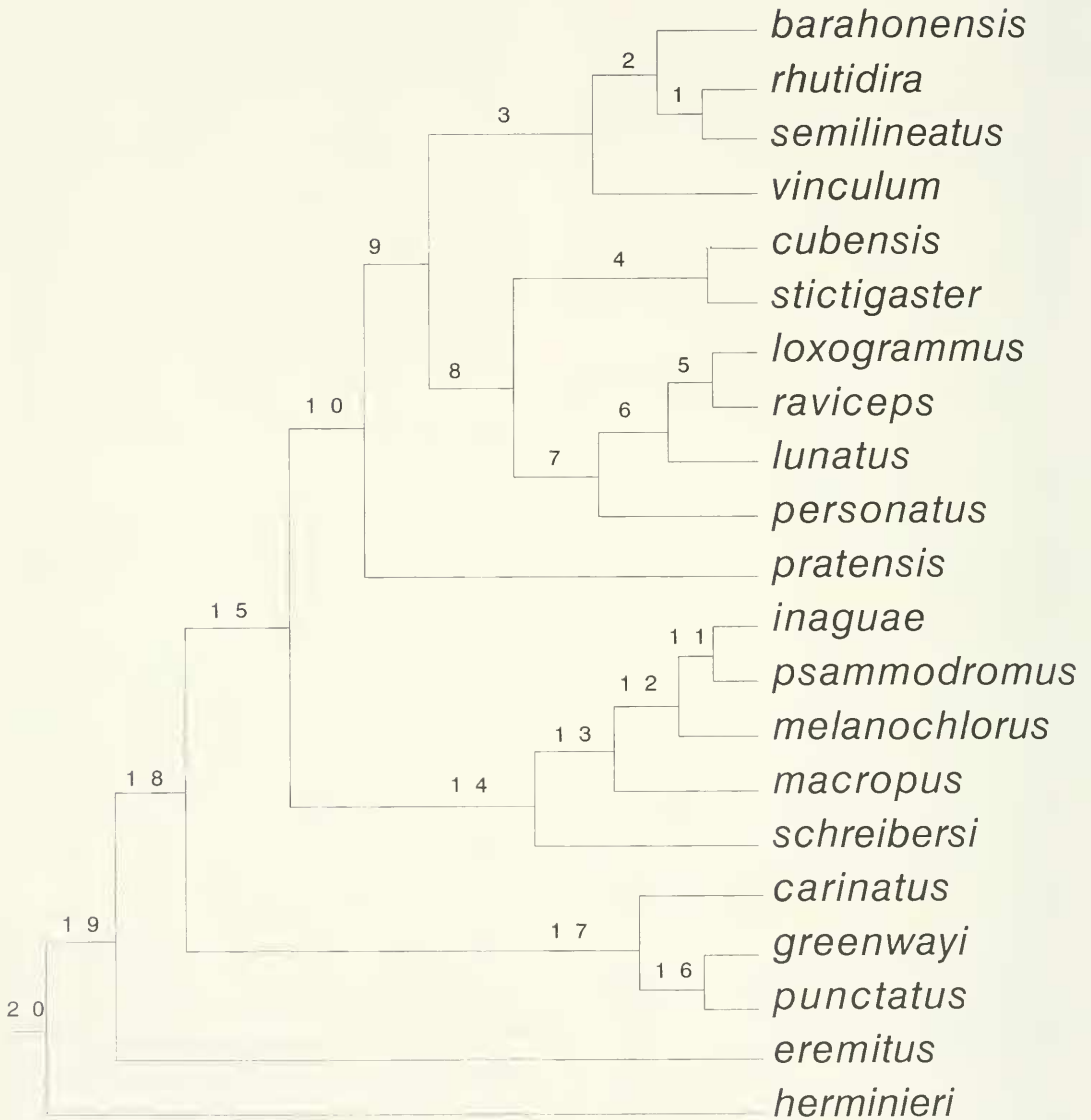


Fig. 15. An alternate tree topology for *Leliocephalus* based on the same data set as Figure 14, but derived from HENNIG86 (length = 118 steps, CI = .44). Support for numbered stems given in text.

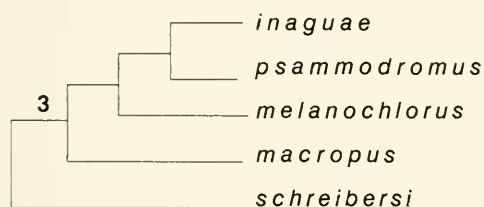
Stems 11–13.—Within the *Leliocephalus melanochlorus* group, *L. macropus* and *schreibersi* are joined at Stem 13 by a Type-II snout scale pattern (16.2; present also in *L. inaguae* and several other species) and by the unique possession of the antegular scale row (32.1). At Stem 12 (*melanochlorus*, *inaguae* + *psammodromus*), the

only unique state is the acquisition of suprascapular blotches (37.1). Additionally, however, the septomaxilla is reduced (6.1; except in *inaguae*; convergent in *loxogrammus* and *herminieri*). The lorilabial scale row increases (21.1; except in *inaguae*; convergent in *eremitus* and *punctatus*). The squamosal acquires a dis-

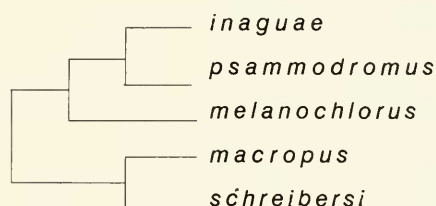
tinct supratemporal process (10.1; convergent in *macropus* and some *loxogrammus*) and the base of the tail is laterally compressed (39.1; also in *herminieri*). Stem 11 (*inaguae* and *psammodromus*) is denoted by the presence of a unique lateral spikelike process above the basal constriction of the premaxillary spine (3.1), by incomplete overlap of the nasals onto the premaxillary spine (1.0), a V-shaped parietal table (8.1; convergent in *loxogrammus*, *greenwayi*, and *punctatus*), the widely homoplastic states of smooth cephalic scales (22.0) and an intermediate number of dorsal crest scales (28.1). Alternate relationships within the *L. melanochlorus* group are shown in Figure 16A–D and discussed below.

Stem 16.—Stem 16 describes a relationship between *Leiocephalus carinatus* and the two southern Bahamian taxa *L. punctatus* and *greenwayi*. Of the three transformations at this node one is unique—the possession of a conspicuously enlarged pair of median frontonasal

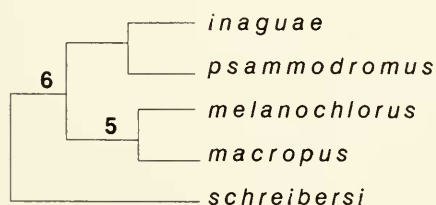
scales (17.1). The others are a shift from complex to moderate antebrachial folds (31.1), and a Type-II snout scale pattern. The relationship between *greenwayi* + *punctatus* (Stem 15) seems odd phenetically because the small body scales and distinct inguinal and scapular patches of *L. greenwayi* contrast sharply with the larger body scales and darker, unicolor pattern of *L. punctatus*. Apart from *L. carinatus*, they possess a V-shaped parietal roof (8.1; convergent with *inaguae* and *psammodromus*) and the plesiomorphic, intermediate state of tricarinate toe scales (30.0). *Leiocephalus greenwayi* and *L. punctatus* converge on the *melanochlorus* group in other ways, but primarily in states that are interpreted as primitive (e.g., incomplete overlap of the premaxillary spine by the nasal bones [1.0]) or for which the polarity is equivocal (e.g., reduced nasal-prefrontal contact [5.1]). Additionally, *L. greenwayi* possesses small body scales (i.e., a high number of dorsal crest scales occiput-vent



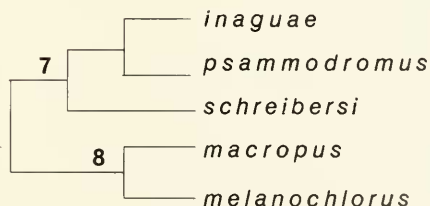
A



B



C



D

Fig. 16. Alternate topologies for species of the *Leiocephalus melanochlorus* group. A is also that of Figure 15 and B that of Figure 14.

[28.1]), a transformation that also characterizes *L. inaguae*, *psammodromus*, *schreibersi*, and *raviceps*, and small lateral trunk scales (26.1). Similarly, *L. punctatus* has a basally constricted premaxillary spine, as do most of the *L. melanochlorus* group, and a frontal that is wide and flat posteriorly, another feature of the *L. melanochlorus* group, and one that also occurs in *L. pratensis*.

Stem 17.—The inclusion of *Leiocephalus eremitus* with *L. carinatus*, and *greenwayi* + *punctatus* at Stem 17 is tenuous owing to the absence of information on *L. eremitus* for the first 15 characters (osteological). *Leiocephalus eremitus* falls out here on the basis of poorly developed tricarinate toe scales (30.0; convergent in *pratensis* and of ambiguous polarity) and the intermediate state of a moderately convex nuchal fold (33.2), which also appears at Stem 8.

Stem 18–19.—In spite of the aforementioned similarities with the *Leiocephalus melanochlorus* group, the Stem 17 clade bears no special relationship to them based on minimum step-transformations. Rather, they configure at Stem 19 as the sister group of all other *Leiocephalus* (except *L. herminieri*) by possessing three internasal scales (20.1). The *L. melanochlorus* group is united at Stem 18 with all of the Stem 10 species by five transformation states, all of which show reversals at higher branches—viz., complete overlap of the nasals onto the premaxillary spine (1.0); nasal-prefrontal contact that obscures the nasal processes of the frontal (5.0); frontal bone wide and flat posteriorly (7.1); cephalic scale ridges present, but restricted (22.1), and the presence of postanal escutcheons (29.1). At this level of the tree, only the presence of postanal escutcheons (29.1) that are absent in *L. carinatus*, *punctatus*, and *greenwayi* (but also absent in *vinculum* and *melanochlorus*) could be a synapomorphy.

Last, there is *Leiocephalus herminieri*, which exhibits no evident affiliation with any other species on the tree. It possesses a peculiar combination of plesiomorphic and apomorphic states that are scattered among other *Leiocephalus* (e.g., reduced septomaxilla, skull rugosities, Type-III pattern of parietal scales, middorsal crest with attenuate scales, strongly convex nuchal fold,

laterally compressed tail base). Only *L. herminieri* possesses keeled ventral scales and retains a large sternum. Also, it is the largest species of *Leiocephalus* known from a whole specimen; several fossil taxa were as large or larger, a fact which engenders anxiety over possible ontogenetic influence on certain osteological characters, despite diligent attempts to correct for size where appropriate. But *L. herminieri* is known from only four specimens, one of which is a skeleton and all of which are adults.

Comments and alternate hypotheses.—Pecus of the character-change list (Appendix III) reveals a low consistency index for numerous transformations, especially those that appear on lower branches of the tree in Figure 14. Accordingly, all the alternate topologies obtained with HENNIG86, which, as mentioned above, affect primarily *Leiocephalus personatus*, *lunatus*, *loxogrammus*, *raviceps*, the *melanochlorus* group, and *eremitus*, are plausible. One of the trees is shown in Figure 15. Note that the major stems are the same as in Figure 14. Further, *L. vinculum* is in a group (Stem 3) with *L. barahonensis* paired to *rhutidira* + *semilineatus*. All taxa except *L. rhutidira* possess a ventromedially placed supratemporal (9.1; convergent in *psammodromus*) and a reversal to smooth cephalic scales (22.0; convergent in *psammodromus* and *inaguae*). Stem 2, uniting *L. rhutidira* and *L. semilineatus* plus *barahonensis*, is specified by the enlarged temporal scale anterodorsal to the ear (23.1). Although unique to this branch, there is, as noted previously, doubt about the homology of the enlarged temporal scale and problems with its variable occurrence in *L. rhutidira* and *L. semilineatus*.

Four alternate topologies for the *Leiocephalus melanochlorus* group (Stem 14) are shown in Figure 16A–D. Each requires reversals or convergences at more inclusive branches, but also frequently with one or, occasionally, two terminal taxa elsewhere, notably *L. herminieri*, *greenwayi*, *punctatus*, and *loxogrammus*. On Stem 3 in Figure 16A, the distal ramus of the squamosal narrows (10.1; also in some *loxogrammus*), the frontal widens and flattens posteriorly (7.1; also in *punctatus* and *pratensis*), the internasals are reduced to two (20.2; a widely homoplastic

character), and cephalic scale ridges extend onto the frontonasals (21.2; also widely homoplastic). Stem 4 (Fig. 16A) is equivalent to Stem 14 of Figures 14 and 15. Stems 5–8 in Figure 16C–D depict the distribution of equally parsimonious alternate states to transformations used to define topology 16A. None of these four topologies is without problems, but topologies 16A and 16B probably would be favored because they afford less disturbance (homoplasy) to characters of “confidence” on other stems.

Of the three options for the placement of

Leiocephalus eremitus, one is shown in Figure 14, the second in Figure 15, and the third is as the sister taxon of all *Leiocephalus* exclusive of *L. carinatus*, *greenwayi*, *punctatus*, and *herminieri* (i.e., it would configure as the sister taxon of Stem 18 in Fig. 14 and of Stem 15 in Fig. 15). Each of these topologies requires broad homoplasy, and probably none should be embraced enthusiastically. Based purely on external morphology because *L. eremitus* was scored only for scales and folds, the suggested affinities of *L. eremitus* lie with the *L. melanochlorus* group.

FOSSIL *LEIOCEPHALUS*

WEST INDIES

Known fossils.—Six species of *Leiocephalus* are known only by fossils from both the Greater and Lesser Antilles. Few of the deposits from which the bones were recovered are associated with accurate chronologies based on radiocarbon ages, but none is likely to be older than late Pleistocene. Some are late Holocene age and include species that became extinct at or near the time of European settlement. Four of these species are extralimital and document that in the recent past *Leiocephalus* ranged throughout all of the main islands of the Greater Antilles and probably most of the islands in the Lesser Antilles at least as far south as Martinique (Fig. 17). Extralimital fossils in the Greater Antilles include one (possibly 2) species from Jamaica, *L. jamaicensis* (Etheridge, 1966b), and two from Puerto Rico, *L. etheridgei* and *L. partitus* (Pregill, 1981). In the Lesser Antilles, the extinct *L. cuneus* (Etheridge, 1964) from Barbuda and Antigua helps to fill an otherwise peculiar distributional gap between the now extinct *L. herminieri*, presumed to have come from Martinique (cf. Species Accounts), and the nearest living species on Hispaniola. With fossils now known from other Leeward and Windward islands (see below), *Leiocephalus* evidently once ranged throughout a good part of the Lesser Antilles.

The two fossil species that are known from deposits located within the current range of *Leiocephalus* are *L. apertosulcus* (Etheridge, 1965) and *L. anonymous* (Pregill, 1984), both

from Hispaniola (Fig. 17). These are the only species of *Leiocephalus* that have an open Meckel's groove. In *L. apertosulcus*, the groove is open and completely exposed medially (Etheridge, 1965), whereas in *L. anonymous*, Meckel's groove is open except at the midpoint of the dentary, at approximately the level of Teeth 12–15 where the groove is closed but not fused (Pregill, 1984). In three other species—*L. etheridgei*, *herminieri*, and *partitus*—Meckel's groove is open below at the level of Teeth 6–8, whence the groove continues as a narrow sulcus to the terminus of the jaw. This condition reflects incomplete fusion as well. Both *L. apertosulcus* and *L. anonymous* have a well-developed intramandibular septum (IMS). Except for *L. cuneus* and *L. partitus*, the intramandibular septum is greatly reduced or absent in all other *Leiocephalus* and in other tropidurids in which Meckel's groove is closed and fused. Previously, I discussed the ambiguous polarity of the open Meckel's groove in *Leiocephalus* and retention of the IMS in *L. cuneus* and *L. partitus* and tentatively concluded that both characters are derived reversals (Pregill, 1984). This still holds under the present scheme with the Tropidurinae being the primary outgroup and the Liolaeminae the second outgroup. The open state occurs in several species of *Liolaemus*.

The extent of emargination at the posterior end of the dentary (12) is difficult to determine because the angular and surangular processes often are incomplete or missing from fossils.

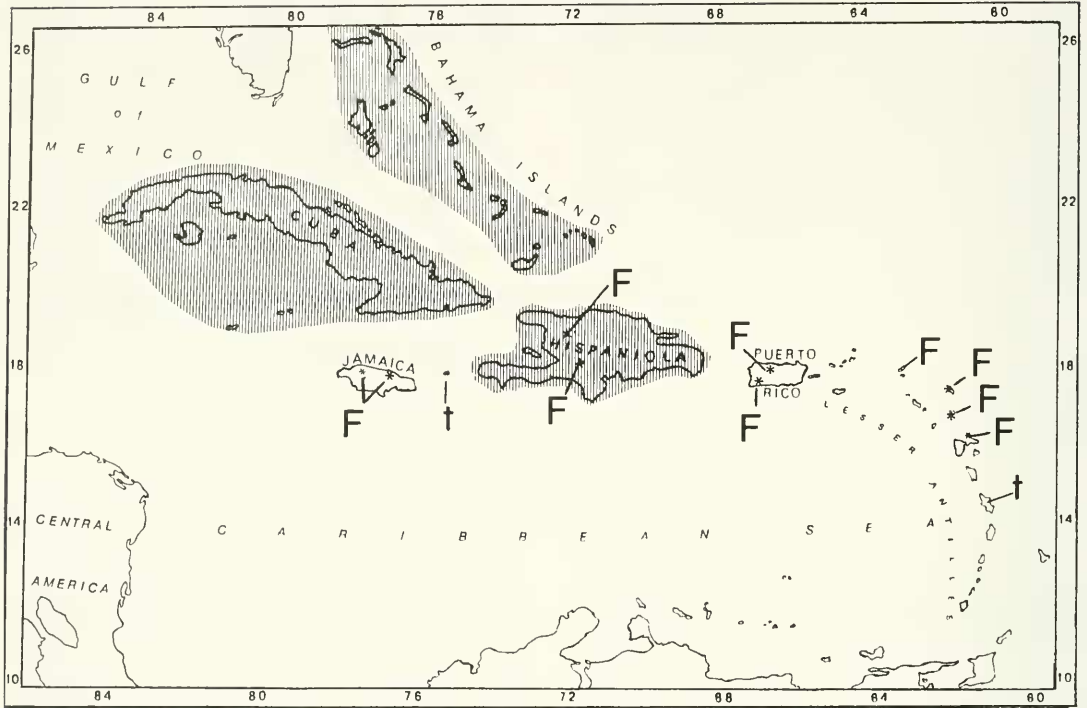


Fig. 17. The West Indies showing the present range (shaded) of *Leiocephalus* and those islands from which the six paleospecies (F) are known (Jamaica, *jamaicensis*; Hispaniola, *anonymous*, *apertosulcus*; Puerto Rico, *etheridgei*, *partitus*; Lesser Antilles, *cuneus*). Two other species (*eremitus* from Navassa Island, and *herminieri* presumably from Martinique) have become extinct historically (†).

Two species, *L. etheridgei* and *L. partitus*, appear to possess the derived condition (12.1).

None of the fossil taxa exhibits the extreme anterior transition to tricuspid teeth (13.1) as in *Leiocephalus rhutidira* and *L. endomychus*, but a transition complete by Tooth 4 or 5 in *L. cuneus* and *L. etheridgei* is within allowable limits of the derived state of that character.

Several fossil species are also represented by cranial elements other than dentaries that can be scored according to the transformations (1–13) in the primary data matrix (Appendix I); these are summarized in Table 3. For three of these transformations, it would be hazardous to estimate character states because articulated skulls are needed for an accurate interpretation. These transformations are, first, the completeness of nasal overlap of the premaxillary spine (1), second, the straight-sided nasal-maxillary suture (4), and, third, the position of the supratemporal (9). In

fossil taxa in which the premaxilla is known (*anonymous*, *cuneus*, and *jamaicensis*), there is indication of neither a constriction at the base of the nasal process (2.1) nor small lateral processes above the constriction (3.1).

Of the five species that have referred frontals, *Leiocephalus anonymous*, *L. apertosulcus*, and *L. cuneus* show evidence that the nasal process of the frontal remained exposed between the prefrontals and nasals (5.1), a transformation that was not polarized. In *L. anonymous*, *etheridgei*, and *jamaicensis* (1 specimen), the frontals are wide and flat posteriorly (7.1) and in *L. anonymous*, *apertosulcus*, *cuneus*, and *jamaicensis* (1 specimen), rugose dermal sculpture is present (11.1). The two frontals referred to *L. jamaicensis* differ in their proportions and degrees of dermal sculpture: possibly, this indicates that more than one species is represented (cf. Species Accounts). None of the fossil frontals has the extensive

Table 3. Some osteological character states for fossil species of *Leiocephalus*. Transformations 1–13 are those from the primary data matrix (text and Appendix I). MG = Meckel's groove (open, open anteriorly, or fused); IMS = intramandibular septum present. A dash (–) indicates that there is no corresponding bone referred, or that the transformation is unascertainable. ? = species assignment questionable for that bone (see text).

Species	Character													MG	IMS
	1	2	3	4	5	6	7	8	9	10	11	12	13		
<i>anonymous</i>	–	0	0	–	1	–	1	0	–	–	1	0	0	2	1
<i>apertosulcus</i>	–	–	–	–	1	–	0	1	–	–	1	0	0	2	1
<i>cuneus</i>	–	0	0	–	1	–	0	1	–	–	1	0	1	0	1
<i>etheridgei</i>	–	–	–	–	0	–	1	–	–	–	0	1	1	1	0
<i>jamaicensis</i>	–	0	0	–	0	–	1?	0	–	–	1?	0	0	0	0
<i>partitus</i>	–	–	–	–	–	–	–	–	–	–	–	1	0	1	1

sculpture seen in such species as *L. barahonensis* and *L. personatus*, which suggests that there might be more than two states to this character.

Of the four species with referred parietals (Table 3), *Leiocephalus apertosulcus* and *L. cuneus* have the strongly V-shaped condition (8.1).

The impact of the addition of the six fossil taxa to the primary data matrix (Appendix 1) on the tree topologies of Figures 14 and 15 is the creation of polytomies at or near terminal branches. The cladogram in Figure 18 is the result of both STRICT and ADAMS Consensus Trees after adding the taxa and data from Table 3. All basal branches of Figures 14 and 15 are preserved. The fossil species (denoted by an asterisk) are clustered among various terminal branches owing to the possession of one or two synapomorphies of a more inclusive group. For example, *L. cuneus*, *L. apertosulcus*, and *L. anonymous* constitute the sister group of *L. greenwayi*, whereas *L. etheridgei* and *L. partitus* are depicted as sister species of *L. schreibersi* in the *L. melanochlorus* group. *Leiocephalus jamaicensis* falls out as the sister taxon of the species above Stem 10 in Figures 14 and 15. With so few applicable data available from the fossils, I am indifferent toward the relationships depicted in Figure 18.

New fossils from the Lesser Antilles.—Fossils collected recently from Anguilla and Guadeloupe represent new island records for *Leiocephalus*. They are described below, and are referred to:

Leiocephalus cf. *L. cuneus*

Anguilla: Center Cave. One partial left dentary, one partial frontal (SDSNH uncat.), by Gregory Pregill, David Steadman, Ronald Crombie, and Linda Gordon, 12 October 1982. Latest Holocene.

Guadeloupe: Grande Terre, unnamed cave at Pnte. du Capucin, ca. 2 km. S Pnte. de la Grande Vigie. One partial left dentary, one maxillary fragment, one sacral vertebra (SDSNH uncat.), by Gregory Pregill, Richard Thomas, and Frank Davis, 14 March 1984. Latest Holocene.

Description: The dentary from Center Cave, Anguilla, is missing its posterior aspect near the level of the last tooth. What remains is 8 mm long. Meckel's groove is open anteriorly as a narrow slit below the most anterior four teeth. An intramandibular septum is present. Most of the teeth remain and all but the four anterior ones have blunt but evidently flared tricuspid crowns. The bone came from an individual with an estimated snout vent length of 65–70 mm.

The dentary from Guadeloupe is missing the anterior tip, but is otherwise complete. With a tooth row of about 12 mm, the bone came from an individual estimated at 110 mm, SVL. The labial surface bears a wedge-shaped scar posteriorly that marks the position of the coronoid overlap in life and extends anteriorly below the most posterior two teeth. There are 19 teeth or alveoli, accounting for the most anterior one or two that

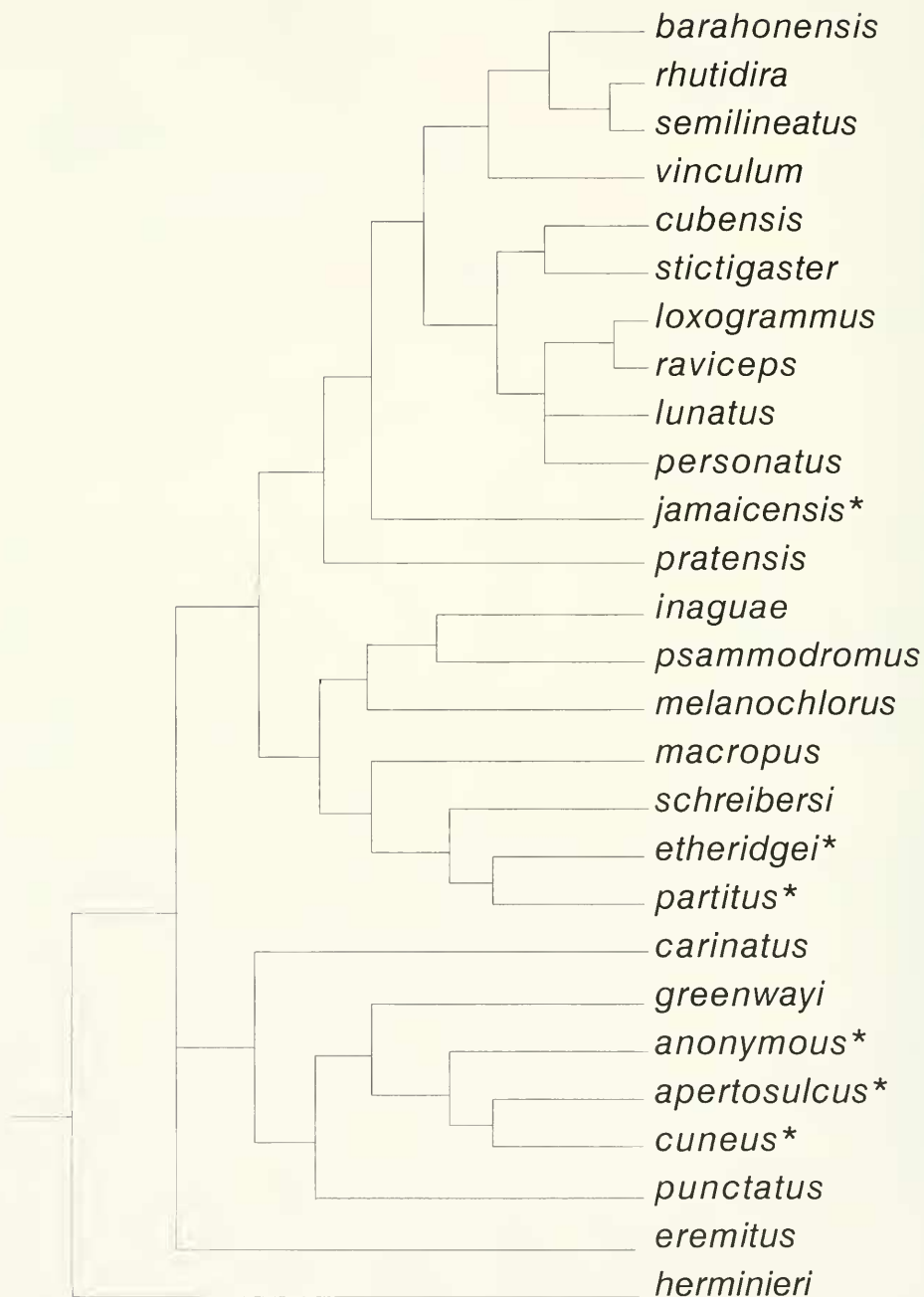


Fig. 18. Consensus tree (STRICT and ADAMS) for *Leiocephalus* with the six fossil species (denoted by asterisk, data from Table 3) added to the primary data matrix (Appendix 1). CF (normalized) = 0.923, CI = 0.484. See text and Figures 14 and 15.

accompanied the broken tip. The transition from simple, pointed crowns to tricuspid crowns is complete at the fifth tooth. The bone is worn and abraded, and incised with what appear to be tooth marks from a small rodent.

Because they are so fragmentary, none of the other three bones requires much comment. The frontal from Center Cave is 8.4 mm long midsagittally, neither wide nor flat posteriorly, and came from an individual with an estimated SVL of 60 mm.

Of the two dentaries, the Guadeloupe specimen is the more nearly complete. Otherwise they differ from one another only in size. Both are small compared with the type series of *Leiocephalus cuneus* from Barbuda (Etheridge, 1964) and the material known from Antigua (Pregill et al., 1988). They are referred to *L. cuneus* on the basis of having (1) an intramandibular septum, (2) a Meckel's groove that is closed and fused except for a shallow sulcus at the anterior end of the jaw, and (3) the transition to tricuspid teeth complete at the fifth tooth. Because *L. cuneus* may have reached a snout-vent length approaching 200 mm, the Anguilla and Guadeloupe specimens (if correctly assigned) must have represented juveniles or subadults. Additional dentaries and other cranial elements would be needed to confirm the identity of the extinct populations on these two islands. Their assignment here is necessarily tentative.

Both the Anguilla and Guadeloupe populations evidently persisted into historical times. The Center Cave material is associated with a radiocarbon age, based on charcoal, of 730 ± 60 yr B.P (Pregill and Steadman, MS). There are no associated dates with the fossils from Pnte. du Capucin, but bones of *Rattus* (a European introduction) were among the remains, all of which were collected from the surface of a shallow ledge.

NORTH AMERICAN TERTIARY

Several fossils from Oligocene and Miocene deposits of North America have been compared with, referred to, or identified as *Leiocephalus*. Most are jaw fragments that have been referred to

the genus on the basis of their having flared tricuspid tooth crowns, a fused Meckel's groove, and, in more nearly complete specimens, an indication of a coronoid labial blade on the dentary. If these fossils were correctly assigned, the presence of *Leiocephalus* in the middle Tertiary of North America would be a curious zoogeographic puzzle indeed, as well as a potentially valuable source of character-state information. However, none of the fossils is diagnostic of *Leiocephalus*, and in fact one referred series probably is better placed with another iguanian taxon.

The oldest of these fossils is a jaw fragment (CM 33650) from the late Oligocene Cedar Ridge Local Fauna of central Wyoming (Setoguchi, 1978:15). This bone is merely a scrap bearing four teeth with unflared crowns. It is far too meager for generic assignment of any sort. Setoguchi's (1978) reference to *Leiocephalus* being based on Estes' (1963) characterization of fossil dentaries from the early Miocene Thomas Farm Locality of Gilchrist County, Florida. The fossils from Thomas Farm consist of two partial dentaries, several jaw fragments, and tentatively associated vertebrae and girdle elements. Characters suggesting *Leiocephalus* are a closed Meckel's groove, a scar marking the overlap of the coronoid labial blade, tricuspid tooth crowns, and pitting at the tooth bases. Referral to *Leiocephalus* was a matter of eliminating other pleurodont iguanians with an open Meckel's groove, those that lacked a coronoid labial blade, or that differed in details of tooth morphology. However, there is nothing diagnostic about them, and being so incomplete their identification necessarily must remain inconclusive.

Robinson and Van Devender (1973) questionably identified as *Leiocephalus* a single anterior half of a right dentary from the Monroe Creek Formation, early Miocene of Nebraska. The specimen has a closed Meckel's groove (except for a large alveolar foramen anteriorly) and a single tricuspid tooth that, based on their illustration (Robinson and Van Devender, 1973:fig. 1D), is only weakly flared at the crown. They compared the fossil in detail with numerous iguanian lizards, but there is nothing about the bone that unambiguously identifies it as *Leiocephalus*.

From the Norden Bridge Quarry, Mio-Plio-

cene Valentine Formation, Nebraska, Estes and Tihen (1964:fig. 5A–B) described a fragment of a right dentary as “Unidentified iguanid, form B.” On the basis of the four teeth with narrow shafts and smoothly flared tricuspid crowns, they concluded that the fossil “... appears to resemble the Recent West Indian iguanid *Leiocephalus* in the general proportions of the teeth and simple flare of the crown (i.e., without thickening of the shaft below the side cusps), but is too incomplete to be identified with any confidence” (Estes and Tihen, 1964:466). I concur.

The largest series of the Tertiary fossils was collected at Annies Geese Cross Quarry in the Lower Valentine Formation of eastern Nebraska (Wellstead, 1982); additionally, there is one left dentary from nearby Railway Quarry B (Holman and Sullivan, 1981). Wellstead (1982) described the numerous partial dentaries and maxillary fragments as a new species, *Leiocephalus septentrionalis*. Because of homonymy with *L. stictigaster septentrionalis* Garrido (1975), the name was emended to *L. nebraskensis* (Wellstead, 1983). Wellstead (1982) also referred to this species the single specimen from the Norden Bridge Quarry described by Estes and Tihen (1964).

The holotype (UNSM 56085) is a nearly complete left dentary with smoothly flared tricuspid teeth, a closed Meckel's groove, and a scar on the posterolabial surface marking the position of the coronoid labial blade in life. *Leiocephalus nebraskensis* was thought to differ from other *Leiocephalus* by its possession of a faintly developed subdental ridge posteriorly and its more robust size. My reexamination of the type series revealed that, aside from shape of the tooth crowns, *L. nebraskensis* lacks critical features of not only *Leiocephalus*, but tropidurids generally. A paratype right dentary (UNSM 47148) is revealing. The dentary-postdentary articulation is entire and the coronoid, the splenial, the anterior half of the angular, and part of the surangular are present. The dentary-postdentary articulation differs from that of *Leiocephalus* in several ways. (1) The posterior end of the dentary terminates below the level of the coronoid apex, rather than extending posteriorly over the surangular. (2) The angular is much larger than in *Leiocephalus* and (3) the splenial is large, trapezoidal, and

terminates posteriorly near the level of the coronoid apex. The splenial of *Leiocephalus* and the Tropidurinae is straplike and extends posteriorly beyond the apex of the coronoid. Some of these differences in the dentary-postdentary articulation also can be deduced from the holotype. The bone is noticeably expanded posterolingually, implying that a large splenial was present and that there was a substantial investiture of the surangular in the dentary-postdentary articulation. The lower jaw of *L. nebraskensis* is actually more characteristic of the iguanid type of architecture described above. Except for tooth crown morphology the fossils could be comfortably assigned to *Dipsosaurus dorsalis*, a conclusion also reached by Norell (1989).

The teeth of *Leiocephalus nebraskensis* have smooth, fleurs-de-lis crowns similar to those of most *Leiocephalus* (and some corytophanids, Lang, 1989). The posterior teeth of *Dipsosaurus dorsalis* have broader crowns, are more laterally compressed, and usually have four cusps. Tricuspid tooth crowns are primitive for iguanines, whereas presence of four or more cusps is thought to be successively derived (de Queiroz, 1987). The posterior teeth of iguanian lizards are highly variable. Among *Leiocephalus* for instance, they may have quite narrow, weakly tricuspid crowns (e.g., *L. partitus*, Pregill, 1981) or may be nearly molariform as in some *L. psammodromus*. In light of this variability, there is no reason to attach special significance to the tricuspid teeth of these Tertiary fossils. For *L. nebraskensis*, the nature of the dentary-postdentary articulation is sufficient to justify removal of this species from *Leiocephalus*.

To summarize, several partial or nearly complete lizard dentaries from middle Tertiary deposits of North America have been referred to, or identified as, *Leiocephalus* on the basis of the possession of flared, tricuspid tooth crowns, a closed Meckel's groove, and a coronoid labial blade. These features are characteristic of *Leiocephalus*, but not unique. In most cases, the referred specimens are too incomplete to assign them confidently to any iguanian taxon. In the case of *Leiocephalus nebraskensis*, it would be more appropriate to refer the taxon to a non-tropidurid genus, perhaps *Dipsosaurus*.

BIOGEOGRAPHY

Leiocephalus is monophyletic and endemic to the West Indies, having been distributed throughout most of the major islands or banks until recently. As a tropidurid iguanian, its ancestry is tied to South America. The radiation of *Leiocephalus* in the West Indies was not explosive like that of *Anolis*, but neither was it insignificant for a terrestrial squamate. The distribution and numbers of species of *Leiocephalus* are comparable to, or greater than, those of other ground-dwelling lizards. For example, diploglossines have about 20 Antillean species, but they do not occur south of Montserrat. *Ameiva* has 18 species ranging throughout the Greater and Lesser Antilles and the Bahamas; however, there is no strong evidence that they constitute a natural group apart from mainland *Ameiva* (but see Barbour and Noble, 1915; Baskin and Williams, 1966). *Leiocephalus* is, of course, the only spiny, scansorial iguanian in the West Indies and most species are xerophilous. The greatest diversity of *Leiocephalus* (12 species) is found on Hispaniola; this is the case for most all other terrestrial reptiles in the Antilles and doubtless is related to the island's size and its habitat diversity. Cuba has six species (with one being extralimital) and the Bahamas five (with all but *L. carinatus* being outside the Great Bank). Puerto Rico has two extinct species, Jamaica one, or possibly two, extinct species, and two, or possibly three, species are known from all of the Lesser Antilles. Only two of the six fossil species are from an island where *Leiocephalus* still exists; all were as large or larger than any extant species.

The earliest West Indian radiation could have begun on any of several islands or banks, whether ancestral *Leiocephalus* originated from over-water dispersal or as a faunal component of a proto-Antillean block. If *Leiocephalus herminieri* is the sister species of all other *Leiocephalus*, its presumed distribution on Martinique suggests a southern entry for the genus into the Antilles, or at least an early presence there. However, *L. herminieri* is not especially plesiomorphic; thus,

one cannot argue persuasively for an application of Hennig's (1966) Progression Rule of character transformation in peripheral isolates (see also Wiley, 1981), especially in the absence of recoverable character information on the extinct species of *Leiocephalus* to the north. Nevertheless, *L. herminieri* is important for understanding the historical distribution of *Leiocephalus*, with or without reference to a center of origin. Similarly, *Leiocephalus carinatus* is in many respects the most generalized and least apomorphic species, and also has the broadest range. It is the only species not endemic to a single island (or bank), being common throughout Cuba, Grand Cayman, Little Cayman, Cayman Brac, and the Great and Little Bahama Banks (Fig. 20).

Indeed, not much is to be gained by hypothesizing an initial center of radiation of *Leiocephalus* in the West Indies, be it Cuba, Hispaniola, the Bahamas, or the Lesser Antilles, because the basal radiation of *Leiocephalus* may be older than the Antilles themselves. If that radiation is not older than the Antilles and if the phylogeny proposed here approximates reality, then Cuba, Hispaniola and the Bahamas have experienced multiple invasions by *Leiocephalus*. The *L. melanochlorus* group, for example, is composed of two southern Bahamian taxa (*psammodromus* and *inaguae*), two Hispaniolan (*melanochlorus* and *schreibersi*) and one Cuban (*macropus*). Another Cuban species, *L. raviceps*, is most closely allied to the Bahamian species *L. loxogrammus* and, together, they belong to an Hispaniolan subgroup (*personatus* and *lunatus*) which inclusively has two additional Cuban members, *L. cubensis* and *L. stictigaster*. This analysis found no strong evidence of a *Leiocephalus personatus*-complex (*personatus*, *lunatus*, *barahonensis*, *vinculum*) in the sense of Cochran (1941) or Schwartz (1967a), but there is some suggestion of other species clusters on Hispaniola (e.g. *rhutidira* + *endomychus* + *semilineatus*).

The distributional patterns of *Leiocephalus* are consistent with the fact that the species compose a group of active, diurnal lizards that evolved

in an archipelago with a complex history of geology and climate (Pregill and Olson, 1981; Williams, 1989). Additionally, there is a comparatively low level of differentiation among species—i.e., a lack of many autapomorphies. One might be persuaded that *Leiocephalus* has not been in the Antilles all that long, if differentiation is a function of time. But such conjecture is hazardous without knowledge of evolutionary rates. Moreover, it could be argued that the habitus of *Leiocephalus* is so like that of all other small, scansorial iguanians (e.g., numerous phrynosomatids and tropidurids) that it must have evolved long ago as a fundamental adaptation, and as an historical constraint, that is the reason for so much similarity among the species.

Leiocephalus has been more vulnerable to extinction and extirpation during the Holocene than any other West Indian squamate, with the possible exception of colubrid snakes (*Alsophis*

spp.). Several factors are probably at play. Elsewhere I suggested that the timing of their extinctions is strongly correlated with human settlement of the islands (Pregill, 1986). Most other squamates have managed to cope at some level with man and his commensals, so why has *Leiocephalus* been so much more prone to extinction? The little we know about the natural history of these lizards suggests that the cause is not a peculiarly restricted diet, because they readily consume a variety of arthropods and, opportunistically, will feed on most anything including plants and other lizards (Schoener et al., 1982; Armas, 1987; pers. obs.). It is possible that some of the species have a relatively low (compared with *Anolis*, for instance) reproductive potential and/or delayed sexual maturity. If so, increased predation by alien species would take its toll, especially in smaller habitat areas.

SPECIES ACCOUNTS

Twenty-nine species of *Leiocephalus* are included in the following accounts. Six of these are fossil species and all are West Indian. One extant species, *L. endomychus*, is proposed as a new combination, and *L. vinculum altavelensis* is reassigned as *L. barahonensis altavelensis*. The accounts are presented alphabetically and include authors, synonymies, holotype, and general statements of distribution (see also Figs. 19–21). For purposes of description, a characterization is provided in place of a strict diagnosis (autapomorphies only). Known subspecies and their authors are included where germane.

LEIOCEPHALUS GRAY (1827)

Holotropis Duméril and Bibron, 1837 (part).

Pristinotus Gravenhorst, 1837.

Steironotus Fitzinger, 1843.

Hispaniolus Cochran, 1928a.

Leiocephalus Etheridge, 1966a.

Type species.—*Leiocephalus carinatus* Gray (1827)

Content.—Twenty-nine species (21 extant; 2 extinct historically; 6 fossil species of late Quaternary age).

Distribution.—West Indies. Now restricted to Cuba, Hispaniola, and the Bahamas. Formerly ranged throughout the Greater Antilles, and Lesser Antilles south to Martinique (Figs. 19–21).

Characterization.—Terrestrial iguanian squamates of small (53 mm SVL) to large (to 200 mm SVL) size; nasal bones large; septomaxilla reduced and free posteriorly; parietal roof constricted posteriorly in adults; nasal process of premaxilla overlapped dorsally and ventrally by nasal bones; Meckel's groove usually closed and fused; tooth crowns variable, but always tricuspid posteriorly; anterior process present on interclavicle; posterior process of interclavicle broadly flared; sternum reduced (except *L. herminieri*); xiphisternal rods curve anteriorly crossing over postxiphisternal ribs; ribs on cervical vertebrae expanded as scoops; caudal neural spine sail-shaped; autonomic fracture planes beginning on fifth or sixth caudal vertebra; cephalic scales large, platelike; enlarged subocular scale present; body scales keeled; ventral scales smooth (except *L. herminieri*); antebrachial folds simple to complex; tail-curling behavior common.



Fig. 19. Principle islands of the West Indies north of Puerto Rico. Extant *Leiocephalus* occur only in Cuba, the Bahamas, and Hispaniola. (See also Figs 17 and 20).

***Leiocephalus anonymous* Pregill, 1984**

Holotype.—USNM(VP) 340182. Right dentary. Type locality: an unspecified cave(s) near St. Michael de l'Atalye, Dépt. L'Artibonite, Haiti. Fossils collected by Arthur J. Poole (ca. 1927) in cave sediment probably no older than latest Pleistocene.

Distribution.—Extinct, known only by fossils from the type locality in Haiti.

Characterization.—Large size (to 130 mm SVL); Meckel's groove open except for a short distance in the middle of the dentary, usually between Teeth 12–15 where the upper and lower borders converge and touch; open portions of Meckel's canal exposing a well-developed intramandibular septum; parietal foramen located wholly within frontal bone.

Remarks.—Pregill (1984) referred numerous dentaries and other cranial elements to this species. He speculated that *L. anonymous* may have persisted into historical times.

***Leiocephalus apertosulcus* Etheridge, 1965**

Holotype.—MCZ(VP) 3404. Right dentary. Type locality: Stratum 2, cave in Cerro de San Francisco, Municipio Pedro Santana, San Rafael (= La Estrelleta) Province, República Dominicana.

Distribution.—Extinct, known only by fossils from the type locality in the Dominican Republic.

Characterization.—Large size (to 150–200 mm SVL); Meckel's groove completely open and exposed on the lingual side of the dentary.



Fig. 20. Distribution of Bahamian species of *Liocephalus*. Islands of the Great and Little Bahama Banks are enclosed at 100 fathoms. See Figure 19 for names of islands.

Remarks.—Etheridge (1965) referred numerous cranial and postcranial bones to this species; its extinction was presumed to be pre-Columbian.

***Liocephalus barahonensis* Schmidt, 1921a**

L. altavelensis Noble and Hassler, 1933.

L. personatus barahonensis —Mertens, 1939; Cochran, 1941.

L. vinculum altavelensis —Schwartz, 1967a.

L. barahonensis —Schwartz, 1967a.

Holotype.—AMNH 2736. Type locality: Barahona, Barahona Province, República Dominicana.

Distribution.—Southcentral Hispaniola, primarily Barahona Peninsula, and west to Jacmel, Dépt. du Sud-Est, Haiti; Isla Beata, Isla Alto Velo.

Characterization.—Moderate size (males to 80 mm, females to 65 mm SVL); nasal overlap of premaxillary spine complete; nasal-maxillary suture curved; nasal processes of frontal not exposed; frontal narrow; parietal table U-shaped in adults; supratemporal ventromedial; supratemporal process of squamosal indistinct; skull roof rugose; angular process of dentary well developed; transition to tricuspid crowns at Tooth 10 or 11 on dentary; snout scale pattern Type III (2 rows of scales between internasals and anterior pair of frontals, with posterior row composed of 3, or a single pair of, enlarged scales); parietal scale pattern Type III (most lateral parietals larger than median pair, postparietals few or absent); 3 internasal scales, usually 2 in contact with rostral; 4 lorilabial scales anterior to enlarged subocular; head scales smooth; single, enlarged

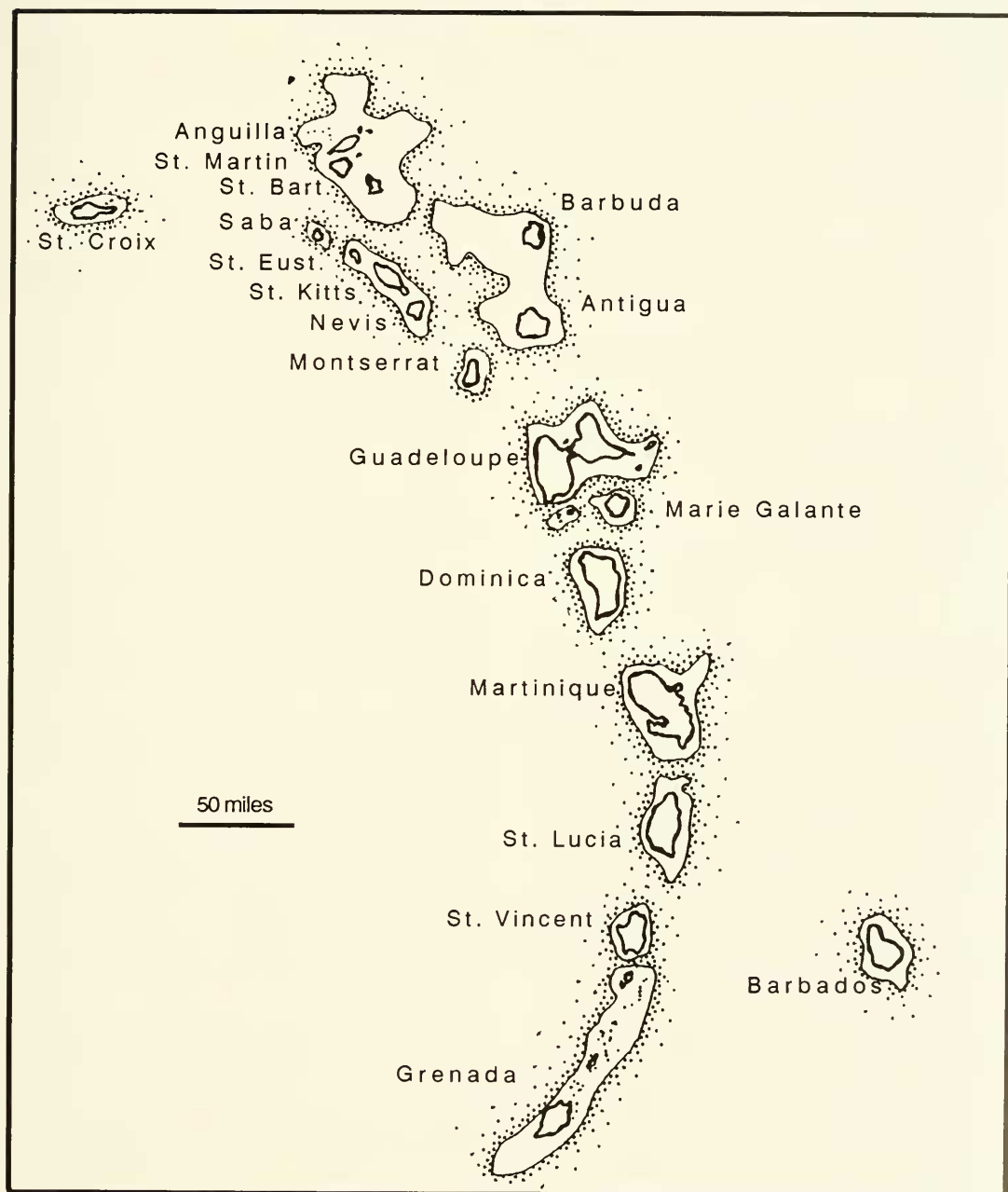


Fig. 21. Islands and banks of the Lesser Antilles. *Leiocephalus herminieri* is thought to have come from Martinique, where it is now extinct. Fossils of *Leiocephalus* are known from (north to south) Anguilla (cf. *cuneus*), Barbuda/Antigua (*cuneus*), and Guadeloupe (cf. *cuneus*). The material from Anguilla and Guadeloupe is new and is described in the text.

temporal scale; lateral neck scales keeled, undifferentiated; lateral trunk scales not reduced; mid-dorsal crest moderate, 42–57 dorsal crest scales occiput–vent; usually 4 postanal escutcheons; tricarinate scales of first and second toe enlarged, forming prominent fringe; lateral neck folds simple; nuchal fold transverse; lateral fold on trunk absent; distinctive scapular or suprascapular pattern absent.

Subspecies.—*barahonensis* Schmidt (1921a); *altavelensis* new combination (see Remarks); *aureus* Cochran (1934b); *beatanus* Noble (1923); *oxygaster* Schwartz (1967a).

Remarks.—Schwartz (1967a) reviewed the subspecies of *Leiocephalus barahonensis* and provided details on scutellation and color pattern based on numerous specimens. He puzzled over the affiliation of *altavelensis*, a population of *Leiocephalus* isolated on Isla Alto Velo off the southern tip of the Barahona peninsula, and suggested that the population might represent (1) an aberrant form of *barahonensis*, (2) a separate species as originally described by Noble and Hassler (1933), or (3) a subspecies of *vinculum*, despite its peculiar distribution far removed from the nearest putative *vinculum* on Ile de la Gonâve. Of these three options, Schwartz (1967a) least preferred the first (as proposed here) because of the smaller size of *altavelensis* and what he regarded as distinct scale and chromatic differences. However, *L. altavelensis* shares with *L. barahonensis* conspicuously enlarged tricarinate toe scales (30); a transverse nuchal fold (33); and a Type III parietal scale pattern (17); in addition, *L. altavelensis* has a moderately enlarged temporal scale (19). Although the polarity of each of these characters is equivocal, none of these states occurs in nominate *vinculum*. Eventually, *L. altavelensis* may prove to be distinct from *barahonensis*, but the available evidence favors the interpretation proposed here.

Leiocephalus carinatus Gray, 1827

Holotropis microlophus Duméril and Bibron, 1837 (part); de la Sagra, 1837.

Leiocephalus macleayii Gray, 1845.

Holotype.—BMNH 1946.8.29.75. Type lo-

cality; restricted by Schwartz and Ogren (1956) to La Habana, Habana Province, Cuba.

Distribution.—Cuba, island-wide and essentially coastal; Isla de la Juventud; Cayman Islands, Great Bahama Bank, Little Bahama Bank; introduced in south Florida and on Great Swan Island.

Characterization.—Large size (males to 130 mm, females to 110 mm SVL); nasal overlap of premaxillary spine usually complete; nasal-maxillary suture curved; nasal processes of frontal exposed in some; frontal narrow; parietal table U-shaped in adults; supratemporal lateral; supratemporal process of squamosal indistinct; skull roof usually smooth; angular process of dentary not well developed; transition to tricuspid crowns at Tooth 10 or 11 on dentary; neural spines of trunk vertebrae obtuse and not expanded distally in some; snout scale pattern Type II (3 rows between internasals and anterior frontals, with posterior row composed of 3 scales in contact with anterior frontals); enlarged pair of frontonasals; parietal scale pattern Type III (most lateral parietals larger than median pair, postparietals few or absent); 3 internasals, usually all in contact with rostral; 4 lorilabial scales anterior to enlarged subocular; cephalic scales smooth; lateral neck scales keeled, undifferentiated; middorsal crest moderate, 43–60 dorsal crest scales occiput–vent; postanal escutcheons absent; tricarinate scales of first and second toe not greatly enlarged, fringe weakly developed; lateral neck folds moderate; nuchal fold moderately convex; lateral fold on trunk absent; distinctive scapular or suprascapular pattern absent.

Subspecies.—*carinatus* Gray; *aquarius* Schwartz and Ogren (1956); *armouri* Barbour and Shreve (1935); *cayensis* Schwartz (1959a); *coryi* Schmidt (1936); *granti* Rabb (1957); *hodsoni* Schmidt (1936); *labrossytus* Schwartz (1959a); *microcyon* Schwartz (1959a); *mogotensis* Schwartz (1959a); *varius* Garman (1887); *virescens* Stejneger (1901); *zayasi* Schwartz (1959a).

Remarks.—Although I examined *Leiocephalus carinatus* from most populations throughout its range, the characterization is based primarily on specimens of *L. c. aquarius* col-

lected from the U.S. Naval Base at Guantánamo Bay. However, Bahamian *L. carinatus* are consistent with respect to these transformations. Some clinal variation in snout-vent length and several meristic features has been demonstrated (Rabb, 1957). Races from mainland Cuba need to be examined carefully and extensively. The Isla de la Juventud population (*L. c. microcyon*), and to some extent those from Little Cayman and Cayman Brac (*L. c. granti*), apparently differ in some skeletal characters (rugose skull, incomplete overlap of nasal process of premaxilla). My samples of these populations were inadequate to assess accurately the significance of these differences.

Leiocephalus cubensis (Gray, 1840)

Tropidurus (Liolaemus) cubensis Gray, 1840.

Holotropis vittatus Hallowell, 1856.

Leiocephalus cubensis—Stejneger, 1917.

Holotype.—BMNH XXIII.98a Type locality: restricted by Schwartz (1959b) to the vicinity of Guanabacoa, Habana Province, Cuba.

Distribution.—Cuba, island-wide but scattered; Isla de la Juventud.

Characterization.—Large size (males to 120 mm, females to 85 mm SVL); nasal overlap of premaxillary spine complete; nasal-maxillary suture curved; nasal processes of frontal not exposed; frontal narrow; parietal table U-shaped in adults; supratemporal lateral; supratemporal process of squamosal indistinct; skull roof rugose; angular process of dentary well developed; transition to tricuspid crowns at Tooth 10 or 11 on dentary; snout scale pattern Type II (3 rows between internasals and anterior frontals, with posterior row composed of 3 scales in contact with anterior frontals); parietal scale pattern Type II (most lateral parietal scales subequal to or slightly larger than median pair, and single row (occasionally 2) of postparietals); 3 internasals, usually 2 in contact with rostral; 4 lorilabial scales anterior to enlarged subocular; cephalic scale ridges extend onto frontonasals; lateral trunk scales not reduced; dorsal crest moderate, 48–64 dorsal crest scales occiput–vent; usually 4 postanal escutcheons; tricarinate scales of first and second toe enlarged, fringe moderate; lateral neck folds

moderate; nuchal fold moderately convex; lateral fold on trunk absent; distinctive scapular and suprascapular pattern absent; facial mask present.

Subspecies.—*cubensis* Gray; *gigas* Schwartz (1959b); *minor* Garrido (in Varona and Garrido, 1970); *pambasileus* Schwartz (1959b); *paraphrus* Schwartz (1959b);

Remarks.—Aggressive behavior in *Leiocephalus cubensis* has been described by Milera (1984), who observed a large male *L. cubensis* repelling a rat that had fled into the lizard's burrow. The same male also was observed seizing an adult male *Anolis sagrei*, presumably as a prey item.

Leiocephalus cuneus Etheridge, 1964

Holotype.—FSM 8226. Left dentary. Type locality: Cave V, Two Foot Bay on the north coast of Barbuda, BWI, by Clayton E. Ray and Robert Allen, 31 March 1963.

Distribution.—Extinct and known only by fossils from Barbuda and Antigua; possibly Anguilla and Guadeloupe (see Remarks).

Characterization.—Large size (to 200 mm SVL); transition from simple to tricuspid tooth crowns complete at Tooth 4 or 5 on dentary, Tooth 3 on maxilla; intramandibular septum present.

Remarks.—Etheridge (1964) referred numerous cranial and postcranial elements to this species, which is known elsewhere on Barbuda from the Indian Town Trail archaeological site (Watters et al., 1984). Abundant remains were also discovered in Burma Quarry fissure (late Holocene) on the adjacent island of Antigua (Steadman et al., 1984; Pregill et al., 1988). Fossils from Anguilla and Guadeloupe also may belong to this species (see above, and Pregill et al., 1988).

Leiocephalus endomychus new combination

Leiocephalus vinculum endomychus Schwartz, 1967a.

Holotype.—MCZ 81099. Type locality: 5.5 km NE Barrage de Péligre, 361 m, Dépt. del'Ouest (de Centre), Haiti, 11 July 1962, by David C. Leber and Albert Schwartz.

Distribution.—Known only from the vicinity of the type locality.

Characterization.—Moderate size (males to 69 mm, females to 56 mm SVL); nasal overlap of premaxillary spine complete; nasal-maxillary suture straight; nasal processes of frontal exposed; frontal narrow; parietal table U-shaped in adults; supratemporal lateral; supratemporal process of squamosal indistinct; skull roof essentially smooth; angular process of dentary well developed; anterior transition to tricuspid crowns at Tooth 3 or 4 on dentary; snout scale pattern Type III (2 rows of scales between internasals and anterior pair of frontals, with posterior row composed of 3, or a single pair of, enlarged scales); parietal scale pattern Type II (most lateral parietal scales subequal to or slightly larger than median pair, and single row [occasionally 2] of postparietals); 3 internasals, usually 2 in contact with rostral; 4 lorilabial scales anterior to enlarged subocular; cephalic scales essentially smooth; enlarged temporal scale usually present; lateral neck scales keeled, undifferentiated; mid-dorsal crest moderate, 51–65 dorsal crest scale occiput–vent; postanal escutcheons numerous, in 3 or 4 rows; tricarinate scales of first and second toe enlarged, fringe moderate; lateral neck folds moderate; nuchal fold moderately convex; lateral fold on trunk absent; distinctive scapular and suprascapular pattern absent.

Remarks.—In his description of *Leiocephalus rhutidira*, Schwartz (1979a) suggested that his new taxon might be properly regarded as a subspecies of *L. vinculum*. His impression was strengthened by the similarities of *L. rhutidira* to the mainland population, *L. v. endomachus*. Chromatic differences, slightly smaller size, and the fact that juveniles and subadults display dorso-lateral stripes were sufficiently compelling differences to treat *L. rhutidira* as specifically distinct. Schwartz (1979a) also was impressed by what he believed were conspicuous lateral neck folds in *L. rhutidira*; hence, the etymology *rhutis* (wrinkled) *deire* (neck). *Leiocephalus vinculum* is polymorphic with respect to the complexity of lateral neck folds (Character 31). Nominate *vinculum* on Ile de la Gonâve have the simple condition (State 2—gular and short antehumeral folds

only), whereas *L. endomachus*, like *L. rhutidira*, possesses the moderate state (State 1—gular, antehumeral and oblique folds). They differ further from nominate *L. vinculum* in sharing a straight-sided nasal-maxillary suture (Character 4.1, as in *L. lunatus* and *L. semilineatus*); exposed nasal processes of the frontal (5.1, several other species also); a laterally placed supratemporal (9.0); the more anterior transition to tricuspid teeth (13.1 unique); the presence (usually) of an enlarged temporal scale dorsolateral to the ear (23.1 as in *barahonensis* and *semilineatus*); and the possession of multiple escutcheon scales (29.2 unique). *Leiocephalus rhutidira* differs from *L. endomachus* by having striped juveniles and greater development of rugosities on the skull roof. These two taxa may be conspecific, but additional specimens from intervening localities in Haiti will need to be studied. For the present, there is ample justification for recognizing *Leiocephalus endomachus* apart from *L. vinculum*, but less justification for placing *L. rhutidira* in the synonymy of *L. endomachus*.

Leiocephalus eremitus Cope, 1868

Leiocephalus (sic) *eremitus* Cope, 1868.

Holotype.—USNM 12016. Type locality: Navassa Island, by W. J. Rasin.

Distribution.—Navassa Island, now extinct; known only by the holotype.

Characterization.—Moderate size (63 mm SVL); angular process of dentary not well developed; transition to tricuspid crowns at Tooth 10 or 11 on dentary; snout scale pattern Type I (3, rarely 4, rows subequal scales between internasals and anterior frontals, none enlarged, posterior row of at least 4 scales in contact with anterior frontals); parietal scale pattern Type III (most lateral parietals larger than median pair, postparietals few or absent); 3 internasal scales, usually all in contact with rostral; 6 lorilabial scales anterior to enlarged subocular; head scales smooth; lateral neck scales small, differentiated; lateral trunk scales not reduced; middorsal crest moderate, 50 dorsal crest scales occiput–vent; tricarinate scales of first and second toe not conspicuously enlarged; lateral neck folds complex;

nuchal fold moderately convex; lateral fold on trunk absent; distinctive scapular or suprascapular pattern absent.

Remarks.—Characterization is based on the only known specimen, a female bearing three mature ova. A purported second specimen was collected by the R. H. Beck expedition in 1917 and later illustrated by Schmidt (1921b). This specimen (AMNH 16919), lacking locality data, was reidentified correctly as *L. melanochlorus* by Thomas (1966) following his visit to Navassa in 1965. Thomas (1966) also provided color notes on the preserved holotype. *Leiocephalus eremitus* is one of several species endemic to this small, limestone island in the Jamaican Channel, about 60 km W Cap des Irois, Haiti.

Leiocephalus etheridgei Pregill, 1981

Holotype.—USNM(VP) 259190. Right dentary. Type locality: Blackbone 1 Cave, 1.2 km S Barrio de Barahona, Municipio de Morovis, Puerto Rico. Late Pleistocene.

Distribution.—Extinct, known only by fossils from the type locality in Puerto Rico.

Characterization.—Large size (to 115 mm SVL); acute, convex ridge present on anterolabial face of dentary below the mental foramina; anterior opening of Meckel's groove extending from the level of Tooth 6 forward to symphysis of jaw.

Remarks.—Pregill (1981) referred other dentaries, cranial bones, and vertebrae to this taxon, one of two species of *Leiocephalus* from Puerto Rico known only by fossils.

Leiocephalus greenwayi Barbour and Shreve, 1935

Holotype.—MCZ 36711. Type locality: East Plana Cay, Bahamas.

Distribution.—Known only from East Plana Cay.

Characterization.—Moderate size (males to 75 mm SVL); nasal overlap of premaxillary spine incomplete; nasal-maxillary suture curved; nasal processes of frontal exposed between prefrontals and nasals; frontal narrow; parietal table narrowly constricted posteriorly, V-shaped in adults;

supratemporal lateral; supratemporal process of squamosal indistinct; skull roof rugose; angular process of dentary not well developed; transition to tricuspid crowns at Teeth 7–9 on dentary; snout scale pattern Type II (3 rows between internasals and anterior frontals, with posterior row composed of 3 scales in contact with anterior frontals); enlarged pair of frontonasals; parietal scale pattern Type III; (most lateral parietals larger than median pair, postparietals few or absent); 3 internasal scales, usually all in contact with rostral; 4 lorilabial scales anterior to enlarged subocular; head scales smooth; lateral neck scales small, differentiated; lateral trunk scales reduced; middorsal crest reduced, 68–70 dorsal crest scales occiput–vent; postanal escutcheons absent; tricarinate scales of first and second toe enlarged, fringe moderate; lateral neck folds moderate; nuchal fold moderately convex; dark supra-axillary and supra-inguinal blotches present.

Remarks.—Little has been written about *Leiocephalus greenwayi* since its original description. Clough and Pulk (1971) listed the species in their synopsis of the vertebrate fauna and vegetation of East Plana Cay. Schwartz (1967b) mentioned, but did not treat, this species in his review of other southern Bahamian *Leiocephalus* (*inaguae* and *psammodromus*). The Plana Cays (= French Cays) are isolated approximately 30 km E Acklins Island.

Leiocephalus herminieri (Duméril and Bibron, 1837)

Holotropis herminieri Duméril and Bibron, 1837.
Leiocephalus herminieri—Boulenger, 1885.

Syntypes.—MNHN 1826, 2389, 6829. Type locality: presumably Martinique (see Remarks). The only other specimen reported in the literature is a skeleton (BMNH 52.12.3.10) received from Paris (Boulenger, 1885); it probably is a syntype also.

Distribution.—Presumably Martinique (see Remarks), now extinct (see Barbour, 1914).

Characterization.—Large size (140 mm SVL); nasal overlap of premaxillary spine incomplete; nasal-maxillary suture curved; nasal

processes of frontal exposed; septomaxilla reduced; frontal narrow; parietal table U-shaped in adults; supratemporal lateral; supratemporal process of squamosal indistinct; skull roof rugose; angular process of dentary not well developed; transition to tricuspid crowns at Tooth 10 or 11 on dentary; snout scale pattern Type I (3, rarely 4, rows subequal scales between internasals and anterior frontals, none enlarged, posterior row of at least 4 scales in contact with anterior frontals); parietal scale pattern Type I (scales small, most lateral parietals smaller than median pair, 2–4 rows postparietals); 4 internasal scales; 4 lorilabial scales anterior to enlarged subocular; cephalic scales smooth; lateral neck scales small, differentiated; lateral trunk scales not reduced; ventral scales keeled; middorsal crest prominent, scales attenuate, 51 dorsal crest scales occiput-vent; postanal escutcheons absent; tricarinate scales of first and second toe enlarged, fringe moderate; lateral neck folds complex; nuchal fold strongly convex; lateral fold on trunk absent; base of tail compressed; distinctive scapular or suprascapular pattern absent.

Remarks.—Several herpetologists have commented on the confusion surrounding Martinique as the type locality for *Leiocephalus herminieri* and other West Indian reptiles (Boulenger, 1885; Stejneger, 1904; Barbour, 1914, 1915; Etheridge, 1964; Baskins and Williams, 1966; Schwartz and Thomas, 1975). The original data accompanying MNHN 2389 indicated that it was collected on “Trinite” by L’Herminier, who sent the specimen to Paris. Whereas “Trinite” could be, and has been (e.g., Barbour, 1914), interpreted as Trinidad, there is a town of Trinité on the north coast of Martinique. Thus, it is not clear whether *Leiocephalus herminieri* was collected on Trinidad or near Trinité, Martinique, or perhaps from both places. The other two specimens, MNHN 1826 and 6829, were collected by Guyon and Plee and are also presumed to have come from Martinique. Martinique was the most active shipping port in the Lesser Antilles during the nineteenth century and, for much of Plee’s material, was merely the transfer point from the field to museums in Europe. For example, Ronald Crombie (in litt.) noted that “A brief search of

taxa described from Plee’s material supposedly coming from Martinique yields the following: *Hylodes martinicensis*, *Ameiva major*, *A. pleei*, *Anolis chlorocyanus*, *A. cristatellus*, *A. marmoratus*, *A. pulchellus*, *Celestus pleei*, *Gonatodes albogularis*, *Sphaerodactylus fantasticus*, and *Amphisbaena caeca*.” In other words, Plee’s collections included species from at least Guadeloupe, Puerto Rico, Hispaniola, and the St. Martin Bank. Some specimens did in fact come from Martinique (*Anolis roquet*), but there is nothing that assures us that *Leiocephalus herminieri* was among these, or is endemic to that island.

A fifth specimen of *Leiocephalus herminieri* was discovered recently by Uno Svensson (pers. comm., 1988) in the Rijksmuseum van Natuurlijke Historie, Leiden. Quite regrettably, it has since been misplaced following spirit removals in the collection (Marinus Hoogmoed, pers. comm., 1989). According to Svensson, the label associated with the specimen read: “*Liocephalus herminieri*, RMNH 2888, Coll: l’Herminier, Mus. Paris, 1835, Trinidad (?), old no: 166.” Svensson measured the snout-vent length at 99 mm, and counted 52 scales around midbody; the ventral scales were keeled. Apparently, l’Herminier must have collected two specimens, one of which was sent to Paris and the other to Leiden.

This is the only species of *Leiocephalus* that possesses keeled ventral scales.

Leiocephalus inaguae Cochran, 1931

Holotype.—USNM 81277. Type locality: Man of War Bay, Great Inagua Island, 08 August 1930, by P. Bartsch.

Distribution.—Great Inagua Island, Bahamas.

Characterization.—Moderately large size (males to 90 mm, females to 74 mm SVL); nasal overlap of premaxillary spine incomplete; premaxillary spine broad at base, constricted, lateral spike above constriction; nasal-maxillary suture curved; nasal process of frontal exposed; frontal wide, flat posteriorly; parietal table narrowly constricted posteriorly, V-shaped in adults; supratemporal lateral; supratemporal process of squamosal indistinct; skull roof smooth; angular

process of dentary not well developed; transition to tricuspid crowns at Teeth 7–9 on dentary; snout scale pattern Type II (3 rows between internasals and anterior frontals, with posterior row composed of 3 scales in contact with anterior frontals); parietal scale pattern Type I (most lateral parietals larger than median pair, postparietals few or absent); 3 internasal scales, usually 2 in contact with rostral; 4 lorilabial scales anterior to enlarged subocular; cephalic scales smooth; lateral neck scales small, differentiated; lateral trunk scales reduced; dorsal crest moderate, 65–77 dorsal crest scales occiput–vent; usually 4 postanal escutcheons; tricarinate scales of first and second toe enlarged, fringe moderate; lateral neck folds complex; nuchal fold strongly convex; lateral fold on trunk; suprascapular blotches conspicuous, continuing down sides and fading.

Remarks.—Aside from the original and then subsequent descriptions by Cochran (1931; 1934c), and later by Schwartz (1967b), there are behavioral and natural history notes on this species by Noble and Klingel (1932), which were based on Klingel's observations when he was shipwrecked on Inagua during the winter of 1930–31 (Klingel, 1932; 1941).

Leiocephalus jamaicensis Etheridge, 1966b

Holotype.—AMNH(VP) 2311. Left dentary. Type locality: Dairy Cave, 2.5 km W Dry Harbour, St. Ann Parish, Jamaica.

Distribution.—Extinct, known only by fossils from Jamaica. Additional fossils are known from Montego Bay Airport Cave at the west end of the air strip, Montego Bay, St. James Parish, and from Portland Ridge Caves, Clarendon Parish (Etheridge, 1966b). Most recently reported by Pregill et al. (1991) from Marta Tick Cave, 8 km WNW Quickstep, Trelawny Parish.

Characterization.—Large size (to 130 mm SVL); pterygoid teeth absent; skull moderately rugose; Meckel's groove closed, fused; anterior border of angular process of articular bone forming an obtuse angle with medial border of articular; main axis of articular process projecting medially from retroarticular condyle (Etheridge, 1966b).

Remarks.—Of the numerous cranial elements and vertebrae referred to this species by Etheridge (1966b), two frontal bones differ from one another in two important ways. The Portland Cave specimen (UF 8496) is wide posteriorly and bears well-developed rugosities. In contrast, the frontal from Montego Bay Airport Cave (UF 8508) is plesiomorphic, being narrow and smooth. Although ontogeny can influence these characters, the two frontals are comparable in size. I think that they represent two species, but which of them is *L. jamaicensis* cannot be determined; the holotype left dentary (AMNH 2311) came from yet a different locality, Dairy Cave. Evidently, *L. jamaicensis*, whether one or two species, was widespread over the central and western part of the island and may have persisted into historical times. The dentaries reported from Marta Tick Cave by Pregill et al. (1991) were unmineralized bones collected from the surface of the cave floor; other fossils that were recovered with them are associated with a C14 age of 770 ± 70 ybp. None of the Type material is believed to be older than latest Pleistocene (Etheridge, 1966b).

Leiocephalus loxogrammus Cope, 1887

Syntypes.—USNM 14569 (3 specimens); MCZ 10931. Type locality: Rum Cay, Bahama Islands, by C. H. Townsend, J. E. Benedict, and Fisher.

Distribution.—Rum Cay and San Salvador (Watling's) Island, Bahamas; possibly Conception Island, Bahamas (see Remarks).

Characterization.—Moderate size (males to 92 mm, females to 74 mm SVL); nasal overlap of premaxillary spine incomplete; nasal maxillary suture curved; nasal processes of frontal exposed; septomaxilla reduced; frontal narrow; parietal table narrowly constricted posteriorly, V-shaped in adults; supratemporal lateral or ventomedial; supratemporal process of squamosal distinct in some; skull roof smooth; angular process of dentary well developed; transition to tricuspid crowns at Teeth 7–9 on dentary; neural processes of trunk vertebrae obtuse, not expanded distally in some; hypapophyses of trunk vertebrae narrow; snout scale pattern Type III (2 rows of scales

between internasals and anterior pair of frontals, with posterior row composed of 3, or a single pair of, enlarged scales); parietal scale pattern Type II (most lateral parietal scales subequal to or slightly larger than median pair, and single row [occasionally 2] of postparietals); enlarged lateral postparietal scale present; 3 internasal scales, usually all in contact with rostral; 4 lorilabial scales anterior to enlarged subocular; cephalic scales ridges restricted; 2 or 3 elongate temporal scales behind eye; lateral neck scales keeled, undifferentiated; lateral trunk scales not reduced; middorsal crest moderate, 55–65 dorsal crest scales occiput–vent; usually 4 postanal escutcheons; tricarinate scales of first and second toe enlarged, fringe moderately developed; lateral neck folds moderate; nuchal fold moderately complex; lateral fold on trunk absent; facial band present.

Subspecies.—*loxogrammus* Cope (Rum Cay); *parnelli* Barbour and Shreve (1935) (San Salvador).

Remarks.—The type series was collected by a party of the U.S. Fish Commission during the cruise of the steamer Albatross, which stopped at San Salvador as well as Rum Cay. There is no compelling reason to doubt Rum Cay as the type locality (Cope, 1887:438), but it is odd that the expedition did not collect *Leiocephalus loxogrammus* on San Salvador where they obtained *Sphaerodactylus* and *Leptotyphlops*. One explanation is that the party confined its field activity to the leeward side in the vicinity of Cockburn Town, the only port on San Salvador. If so, their failure to collect *L. loxogrammus* accords with distributional records of Olson et al. (1990), who found that the species was nearly restricted to the opposite (windward) side of the island. They also reported Holocene fossils of *L. loxogrammus* from several sinkholes located in the southern and eastern sections of San Salvador.

A population of *Leiocephalus loxogrammus* may exist on Conception Island northwest of Rum Cay, but as yet, it has not been verified with specimens (Schwartz et al., 1978).

Leiocephalus lunatus Cochran, 1934a

Leiocephalus personatus lunatus Cochran, 1934a.
Leiocephalus lunatus—Schwartz, 1967a.

Holotype.—FMNH 166. Type locality: Santo Domingo, Distrito Nacional, República Dominicana.

Distribution.—Southern and eastern Dominican Republic, primarily coastal; Isla Saona, Isla Catalina.

Characterization.—Small to moderate size (males to 67 mm, females to 60 mm SVL); nasal overlap of premaxillary spine complete or not; nasal-maxillary suture straight; nasal processes of frontal not exposed; frontal narrow; parietal table U-shaped in adults; supratemporal lateral; supratemporal process of squamosal indistinct; skull roof rugose; angular process of dentary not well developed; transition to tricuspid crowns at Teeth 7–9 on dentary; hypapophyses of posterior trunk vertebrae usually narrow; snout scale pattern Type III (2 rows of scales between internasals and anterior pair of frontals, with posterior row composed of 3, or a single pair of, enlarged scales); parietal scale pattern Type II (most lateral parietal scales subequal to or slightly larger than median pair, and single row [occasionally 2] of postparietals); enlarged lateral postparietal scale present; 3 internasal scales, usually 2 in contact with rostral; 4 lorilabial scales anterior to enlarged subocular; cephalic scale ridges restricted; moderately enlarged temporal scale present in some; lateral neck scales keeled, undifferentiated; lateral trunk scales not reduced; middorsal crest prominent, scales attenuate, 50–68 dorsal crest scale occiput–vent; usually 4 postanal escutcheons; tricarinate scales of first and second toe enlarged, fringe moderate; lateral neck folds moderate; nuchal fold moderately convex; lateral fold on trunk absent; supraaxillary blotch in males; distinct spotting on chin and throat.

Subspecies.—*lunatus*, Cochran (1934a); *arenicolor* Mertens (1939); *lewisi* Schwartz (1967a); *louisae* Cochran (1934b); *melaenascelis* Schwartz (1967a); *thomasi* Schwartz (1967a).

Remarks.—Considerable variation in skeletal and integumentary (squamation) characters calls for a closer examination of this species. The most detailed descriptions are those of Cochran (1934a,b; 1941) and especially Schwartz (1967a).

***Leiocephalus macropus* Cope, 1863**

Liocephalus (sic) *macropus* Cope, 1863.

Leiocephalus macropus—Stejneger, 1917.

Lectotype.—USNM 25819, selected by Hardy (1958a); syntypes MCZ 10930; USNM 12254, 25819-23, 25825-29 (see Remarks). Type locality: restricted by Stejneger (1917) to Monte Verde, Guantánamo Province, Cuba (but see Remarks).

Distribution.—Cuba, from Pinar del Río east, but primarily eastern Cuba.

Characterization.—Moderate to large size (males to 92 mm, females to 75 mm SVL); nasal overlap of premaxillary spine complete; base of nasal process of premaxilla broad; nasal-maxillary suture curved; nasal processes of frontal exposed; frontal broad and flat posteriorly; parietal table U-shaped in adults; supratemporal lateral; supratemporal process of squamosal usually distinct; skull roof smooth; angular process of dentary not well developed; transition to tricuspid crowns at Tooth 10 or 11 on dentary; snout scale pattern Type II (3 rows between internasals and anterior frontals, with posterior row composed of 3 scales in contact with anterior frontals); parietal scale pattern Type I (scales small, most lateral parietals smaller than median pair, 2-4 rows postparietals); usually 2 internasal scales; 4 lorilabial scales anterior to enlarged subocular; cephalic scale ridges extend onto frontonasals; lateral neck scales small, differentiated; lateral trunk scales reduced; middorsal crest moderate, 50-73 dorsal crest scales occiput-vent; usually 4 postanal escutcheons; tricarinate scales of first and second toe enlarged, fringe moderate; lateral neck folds complex; nuchal fold strongly convex; lateral fold on trunk present; supraaxillary blotch present, bisected by white vertical bar; dark facial band extending onto trunk.

Subspecies.—*macropus* Cope (1863); *aegialus* Schwartz and Garrido (1967); *asbolonus* Schwartz and Garrido (1967); *felinoi* Garrido (1979); *hoplites* Zug (1959); *hyacinthurus* Zug (1959); *immaculatus* Hardy (1958a); *koopmani* Zug (1959); *lenticulatus* Garrido (1973b); *phylax* Schwartz and Garrido (1967); *torrei* Garrido (1979).

Remarks.—Schwartz and Garrido (1967) determined that the presumed syntypes (Cochran,

1961) of *Leiocephalus macropus* might not have been the material Cope had in front of him when he described this species. For example, the supposed syntypes also included a specimen of *L. raviceps*, which Cope (1863) himself assuredly could have distinguished because he described that species in the same paper. Moreover, Hardy's (1958a) selection of USNM 25819 as the lectotype was based on the assertion that that specimen best fit Cope's description. However, this is not the case, which casts further doubt on the veracity of the type series. Hence, restricting the type locality to Monte Verde (Stejneger, 1917) becomes moot, as the USNM series likely was collected from several stations in eastern Cuba (Schwartz and Garrido, 1967).

Leiocephalus macropus displays considerable clinal variation in pattern and scutellation throughout its range (see also Hardy, 1958b).

***Leiocephalus melanochlorus* Cope, 1863**

Syntypes.—MCZ 3598; USNM 53402; CAS 39392. Type locality: near Jérémie, Dépt. de la Grand'Anse, Haiti.

Distribution.—Southern Haiti, essentially the Tiburon Peninsula; Ile-à-Vache.

Characterization.—Large size (males to 130 mm, females to 102 mm SVL); nasal overlap of premaxillary spine complete; nasal-maxillary suture straight; nasal processes of frontal exposed; septomaxilla reduced; frontal broad and flat posteriorly; parietal table U-shaped in adults; supratemporal lateral; supratemporal process of squamosal distinct; skull roof smooth; angular process of dentary not well developed; transition to tricuspid crowns at Tooth 10 or 11 on dentary; snout scale pattern Type I (3, rarely 4, rows subequal scales between internasals and anterior frontals, none enlarged, posterior row of at least 4 scales in contact with anterior frontals); parietal scale pattern Type I (scales small, most lateral parietals smaller than median pair, 2-4 rows postparietals); usually 2 internasal scales; 6 lorilabial scales anterior to enlarged subocular; cephalic scale ridges extend onto frontonasals; body scales large; lateral neck scales small, differentiated; lateral trunk scales reduced; middor-

sal crest moderate, 37–53 dorsal crest scales occiput–vent; postanal escutcheons absent; tricarinate scales of first and second toe enlarged; fringe moderate; lateral neck folds complex; nuchal fold strongly convex; lateral fold on trunk present; suprascapular blotches present, continuing onto trunk; tail compressed at base.

Subspecies.—*melanochlorus* Schwartz (1965); *hypsistus* Schwartz (1965).

Leiocephalus onaneyi Garrido, 1973a

Holotype.—IZ-2869. Type locality: the top of Loma de Mocamba, between San Antonio del Sur and Imías, Oriente (Guantánamo) Province, Cuba.

Distribution.—Known only from the type locality, but presumed to occur in the hills of the Sierra de Imías.

Characterization.—Moderate size (73 mm SVL); belly and throat white, without spots, reticulations, or marks; dorsum with eight well-delimited zones of alternating white and chocolate; (median) parietal scales only in contact posteriorly; supraorbital semicircles incomplete; 48 dorsal crest scales occiput–vent; five loreals; 4 or 5 supralabials and an equal number of infralabials.

Remarks.—Besides the holotype, an adult female, only two other specimens of *Leiocephalus onaneyi* have been reported, the paratypes listed by Garrido—a male (IZ 2848) and juvenile female (IZ 2870). The characterization above is taken directly from Garrido's diagnosis and, therefore, is not comparable to other species accounts in this section. In his comparison with other Cuban *Leiocephalus*, Garrido (1973a) commented that only *L. stictigaster* would likely be confused with *L. onaneyi*, but that they differed in the immaculate throat and the distinct dorsum of eight zones (6 less distinct zones in *L. stictigaster*). From the accompanying photographs in Garrido (1973a), *L. onaneyi* indeed gives the impression of an aberrant *L. stictigaster*. The cephalic scales seem to have well-defined ridges extending onto the frontonasals.

Leiocephalus onaneyi is restricted to a small region of sharp karst topography characterized

by low rainfall and a high level of endemic, xerophytic vegetation.

Leiocephalus partitus Pregill, 1981

Holotype.—USNM(VP) 259203. Right dentary. Type locality: Guánica Bat Cave, Reserva Forestal Guánica, 6 km E Barrio de Guánica, Municipio de Guayanilla, Puerto Rico.

Distribution.—Extinct, known only by fossils from the type locality, and from Cueva del Perro, Municipio de Morovis, Puerto Rico (Pregill, 1981).

Characterization.—Large size (estimated SVL 125–130 mm); dentary with a well-developed intramandibular septum; tooth crowns narrow and weakly flared; Meckel's groove closed and fused except from below the seventh tooth to the anterior tip of the jaw.

Remarks.—Only two fossils of this species are known, the holotype and another right dentary (KUPV 11473) from Cueva del Perro. The two fossil localities are on opposite sides of the island from one another in northcentral and southwest Puerto Rico, respectively. Although no radiocarbon ages are available for either of these deposits, they are most likely late Pleistocene to Holocene age (Pregill, 1981).

Leiocephalus personatus Cope, 1863

Leiocephalus (sic) *trigeminatus* Cope, 1863.

Leiocephalus personatus—Cochran, 1932 (part).

Leiocephalus personatus—Schwartz, 1967a.

Syntype.—MCZ 3615. Type locality: near Jérémie, Dépt de la Grand' Anse, Haiti. The holotype of *Leiocephalus trigmenatus* is lost (formerly in MCZ).

Distribution.—Island-wide on Hispaniola, especially northern Dominican Republic.

Characterization.—Moderate size (males to 86 mm, females to 63 mm SVL); nasal overlap of premaxillary spine complete; nasal-maxillary suture curved; nasal process of frontal exposed in some; frontal narrow; parietal table U-shaped in adults; supratemporal lateral; supratemporal process of squamosal indistinct; skull roof rugose; angular process of dentary well developed; tran-

sition to tricuspid crowns at Tooth 10 or 11 on dentary; hypapophyses of trunk vertebrae usually narrow; snout scale pattern Type III (2 rows of scales between internasals and anterior pair of frontals, with posterior row composed of 3, or a single pair of, enlarged scales); parietal scale pattern Type II (most lateral parietal scales subequal to or slightly larger than median pair, and single row [occasionally 2] of postparietals); 3 internasal scales, usually 2 in contact with rostral; 4 lorilabial scales anterior to enlarged subocular; cephalic scale ridges extend onto frontonasals; moderately enlarged temporal scale present in some; lateral neck scales undifferentiated; lateral trunk scales not reduced; mid-dorsal crest prominent, scales attenuate, 41–64 dorsal crest scales occiput–vent; usually 4 postanal escutcheons; tricarinate scales of first and second toe enlarged, fringe moderately developed; lateral neck folds moderate; nuchal fold moderately convex; antegular scale fold present in some; lateral fold on trunk absent; ventral pattern absent in males, females often with dark spotting on throat and chest; facial mask usually evident.

Subspecies.—*personatus* Cope (1863), Barbour (1935, with which Barbour was tempted to lump *L. herminieri*); *actites* Schwartz (1967a); *agraulus* Schwartz (1967a); *budeni* Schwartz (1967a) *elattoprosopon* Gali, Schwartz, and Suarez (1988); *mentalis* Cochran (1932); *poikilometes* Schwartz (1969); *pyrrholaemus* Schwartz (1971); *scalaris* Cochran (1932); *pulcherrimus* Mertens (1939); *socoensis* Gali and Schwartz (1982); *tarachodes* Schwartz (1967a); *trujilloensis* Mertens (1939).

Remarks.—*Leiocephalus personatus* is an especially variable species, as demonstrated by the numerous populations given subspecific designation, and in the character discordance noted above. A more detailed examination of this widespread Hispaniolan taxon is warranted.

***Leiocephalus pratensis* (Cochran, 1928a)**

Hispaniolus pratensis Cochran, 1928a.

Leiocephalus pratensis Etheridge, 1966a.

Holotype.—USNM 69189. Type locality: Atalaye Plantation near St. Michel, Dépt du Nord, Haiti; emended by Schwartz (1968) to Atalaye

Plantation near St.-Michel de l'Atalaye, Dépt de l'Artibonite, Haiti.

Distribution.—Known only from the vicinity of the type locality, and from Ile à Cabrit in the Golfe de la Gonâve.

Characterization.—Small to moderate size (males to 64 mm, females to 55 mm SVL); nasal overlap of premaxillary spine complete; nasal-maxillary suture curved; nasal processes of frontal not exposed; frontal wide and flat posteriorly; parietal table U-shaped in adults; supratemporal lateral; supratemporal process of squamosal indistinct; skull roof smooth; angular process of dentary not well developed; transition to tricuspid crowns at Tooth 10 or 11 on dentary; snout scale pattern Type III (2 rows of scales between internasals and anterior pair of frontals, with posterior row composed of 3, or a single pair of, enlarged scales); parietal scale pattern Type III (most lateral parietals larger than median pair, postparietals few or absent); usually 2 internasal scales; 4 lorilabial scales anterior to enlarged subocular; supraocular scales usually 5/5; cephalic scale ridges restricted; lateral neck scales keeled, undifferentiated; lateral trunk scales not reduced; middorsal crest absent; usually 4 postanal escutcheons; lenticular scale organs absent; tricarinate scales of first and second toe not enlarged, fringe weakly developed; lateral neck folds simple; nuchal fold transverse; lateral fold on trunk absent; distinctive scapular or suprascapular pattern absent.

Subspecies.—*pratensis*, Cochran (1928a); *chimarus* Schwartz (1979b).

***Leiocephalus psammodromus* Barbour, 1916a**

Liocephalus (sic) *arenarius* Barbour, 1916a.

Leiocephalus psammodromus Barbour, 1920 (substitute name for *arenarius*, preoccupied by *Steironotus* [*Ophryoessoides*] *arenarius* Tschudi, 1845).

Holotype.—MCZ 11948. Type locality: "Bastion Cay," Turks Island, B.W.I., by L. L. Mowbry.

Distribution.—Turks and Caicos Islands: scattered on associated Cays.

Characterization.—Large size (males to 105 mm, females to 84 mm SVL); nasal overlap of

premaxillary spine incomplete; premaxillary spine broad, constricted at base and with spikelike lateral process; nasal-maxillary suture curved; nasal processes of frontal exposed; septomaxilla reduced; frontal broad and flat posteriorly; parietal table narrowly constricted posteriorly, V-shaped in adults; supratemporal ventromedial; supratemporal process of squamosal distinct; skull roof smooth; angular process of dentary not well developed; transition to tricuspid crowns at Tooth 10 or 11 on dentary; snout scale pattern Type I (3, rarely 4, rows subequal scales between internasals and anterior frontals, none enlarged, posterior row of at least 4 scales in contact with anterior frontals); parietal scale pattern Type I (scales small, most lateral parietals smaller than median pair, 2–4 rows postparietals); usually 4 internasal scales; 5 or 6 lorilabial scales anterior to enlarged subocular; cephalic scales essentially smooth; lateral neck scales small, differentiated; lateral trunk scales reduced middorsal crest moderate, 56–81 dorsal crest scales occiput–vent; body scales small; 2–4 postanal escutcheons occasionally present; tricarinate scales of first and second toe enlarged, fringe moderate; lateral neck folds complex; nuchal fold strongly convex; lateral fold on trunk present; suprascapular blotches present; base of tail laterally compressed.

Subspecies.—*psammodromus* Barbour (1920), Schwartz and Thomas (1975); *aphretor* Schwartz (1967b); *apocrinus* Schwartz (1967b); *cacodoxus* Schwartz (1967b); *hyphantus* Schwartz (1967b); *mounax* Schwartz (1967b).

Remarks.—The type locality, “Bastion Cay,” cannot be located on maps. *Leiocephalus psammodromus* is a variable species that would benefit from further taxonomic study. Holocrine glands of this species were described by Alexander and Maderson (1972).

Leiocephalus punctatus Cochran, 1931

Leiocephalus carinatus punctatus Cochran, 1931.

Leiocephalus carinatus helenae Barbour and Shreve, 1935.

Leiocephalus carinatus picinus Barbour and Shreve, 1935.

Leiocephalus punctatus—Etheridge, 1966a (as suggested by Rabb, 1957).

Holotype.—USNM 81560. Type locality: North shore of the bay at Jamaica Wells, Acklin’s Island, Bahamas.

Distribution.—Crooked-Acklins Bank, Samana (Atwood) Cay.

Characterization.—Moderate size (males to 78 mm SVL); nasal overlap of premaxillary spine incomplete; premaxillary spine broad, constricted at base; nasal-maxillary suture curved; nasal processes of frontal exposed; frontal broad and flat posteriorly; parietal table narrowly constricted posteriorly, V-shaped in adults; supratemporal ventromedial; supratemporal process of squamosal indistinct; skull roof smooth; angular process of dentary not well developed; transition to tricuspid crowns at Tooth 10 or 11 on dentary; snout scale pattern Type II (3 rows between internasals and anterior frontals, with posterior row composed of 3 scales in contact with anterior frontals); enlarged median pair of frontonasals; parietal scale pattern Type III (most lateral parietals larger than median pair, postparietals few or absent); 3 internasals, usually 2 in contact with rostral; 5 or 6 lorilabial scales anterior to enlarged subocular; cephalic scales smooth; moderately enlarged temporal scale in some; lateral neck scales small, differentiated; lateral trunk scales not reduced; middorsal crest moderate, 49–59 dorsal crest scales occiput–vent; postanal escutcheons absent; tricarinate scales of first and second toe enlarged, fringe moderate; lateral neck folds moderate; nuchal fold moderately convex; lateral fold on trunk absent; scapular or suprascapular pattern absent; distinctive light spotting on head.

Remarks.—Meristic and morphometric details of this species were treated by Rabb (1957).

Leiocephalus raviceps Cope, 1863

Syntypes.—ANSP 8601–03; MCZ 10928; USNM 4162. Type locality: Eastern Cuba; restricted by Gundlach (1880) to the mountains near Guantánamo, Oriente.

Distribution.—Primarily eastern half of Cuba, but disjunct populations in Matanzas and Pinar del Río Provinces.

Characterization.—Moderate size (males to 72 mm, females to 60 mm SVL); nasal overlap of premaxillary spine complete; nasal maxillary suture curved; nasal processes of frontal not exposed; frontal narrow; parietal table U-shaped in adults; supratemporal lateral; supratemporal process of squamosal indistinct; skull roof rugose; angular process of dentary well developed; transition to tricuspid crowns at Tooth 10 or 11 on dentary; neural processes of trunk vertebrae at obtuse angle, not distally expanded; hypapophyses of trunk vertebrae narrow; snout scale pattern Type III (2 rows of scales between internasals and anterior pair of frontals, with posterior row composed of 3, or a single pair of, enlarged scales); parietal scale pattern Type II (most lateral parietal scales subequal to or slightly larger than median pair, and single row [occasionally 2] of postparietals); enlarged postparietal scale laterally; 3 internasals, usually 2 in contact with rostral; 4 lorilabial scales anterior to enlarged subocular; cephalic scale ridges extend onto frontonasals; 2 or 3 elongate temporal scales behind eye; lateral neck scales keeled undifferentiated; lateral trunk scales not reduced; middorsal crest moderate, 55–74 dorsal crest scales occiput–vent; usually 4 postanal escutcheons; tricarinate scales of first and second toe enlarged, fringe moderate; lateral neck folds moderate; nuchal fold moderately convex; lateral fold present on trunk; dark facial band present, extending onto trunk.

Subspecies.—*raviceps* Cope (1863), Schwartz (1960b); *delavarai* Garrido (1973b); *jaumei* Schwartz and Garrido (1968b); *klinikowski* Schwartz (1960b); *uzzelli* Schwartz (1960b).

Leiocephalus rhutidira Schwartz, 1979a

Holotype.—CM 60520. Type locality: Lapierre, 10.6 km W Çà Soleil, Dépt. de l'Artibonite, Haiti.

Distribution.—Known only from the type locality.

Characterization.—Small size (males to 66 mm, females to 57 mm SVL); nasal overlap of premaxillary spine complete; nasal-maxillary suture straight; nasal processes of frontals ex-

posed; frontal narrow; parietal table U-shaped in adults; supratemporal lateral; supratemporal process of squamosal indistinct; skull roof rugose; angular process of dentary well developed; transition to tricuspid crowns at Tooth 3 or 4 on dentary; snout scale pattern Type III (2 rows of scales between internasals and anterior pair of frontals, with posterior row composed of 3, or a single pair of, enlarged scales); parietal scale pattern Type II (most lateral parietal scales subequal to or slightly larger than median pair, and single row [occasionally 2] of postparietals); 3 internasals, usually 2 in contact with rostral; 4 lorilabial scales anterior to enlarged subocular; cephalic scales essentially smooth; enlarged temporal scale usually present; lateral neck scales keeled, undifferentiated; lateral trunk scales not reduced; middorsal crest moderate, 51–65 dorsal crest scale occiput–vent; postanal escutcheons numerous in 3 or 4 rows; tricarinate scales of first and second toe enlarged, fringe moderate; lateral neck folds moderate; nuchal fold moderately convex; lateral fold on trunk absent; scapular or suprascapular pattern absent; juveniles with striped dorsum.

Remarks.—See account of *Leiocephalus endomychus*.

Leiocephalus schreibersi (Gravenhorst, 1837)

Pristinotus schreibersi Gravenhorst, 1837.

Steironotus schreibersi—Fitzinger, 1843.

Leiocephalus schreibersi—Cope, 1868.

Holotype.—Unlocatable, apparently deposited in Breslau Museum; Type locality: “San Domingo”; restricted by Schwartz (1968) to the vicinity of Port-au-Prince, Dépt. de l'Ouest, Haiti.

Distribution.—Fairly widely scattered north to south in central Hispaniola, but absent from large areas of the interior, west to Port-au-Prince; Ile de la Tortue; introduced in south Florida.

Characterization.—Moderately large size (males to 107 mm females to 78 mm SVL); nasal overlap of premaxillary spine complete, premaxillary spine wide, constricted at base; nasal-maxillary suture curved; nasal processes of frontal not exposed; frontal narrow; parietal table U-shaped in adults; supratemporal lateral; supra-

temporal process of squamosal indistinct; skull roof smooth; angular process of dentary well developed; transition to tricuspid crowns at Tooth 10 or 11 on dentary; neural processes of trunk vertebrae at obtuse angle, not expanded distally; clavicle narrow; snout scale pattern Type II (3 rows between internasals and anterior frontals, with posterior row composed of 3 scales in contact with anterior frontals); parietal scale pattern Type I (scales small, most lateral parietals smaller than median pair, 2–4 rows postparietals); 3 internasal scales, usually 2 in contact with rostral; 4 lorilabial scales anterior to enlarged subocular; cephalic scale ridges restricted; lateral neck scales small, differentiated; lateral trunk scales reduced; middorsal crest small, 63–87 dorsal crest scales occiput–vent; usually 4 postanal escutcheons; tricarinate scales of first and second toe enlarged, fringe moderate; lateral neck folds complex; nuchal fold strongly convex; lateral fold present on trunk; 5–7 transverse rows of dark, contrasting scales on venter; scapular or suprascapular pattern absent.

Subspecies.—*schreibersi* Gravenhorst (1837), Schwartz (1968); *nesomorus* Schwartz (1968).

Remarks.—Aspects of the thermal biology of *L. schreibersi* were described by Marcellini and Jenssen (1989).

***Leiocephalus semilineatus* Dunn, 1920**

Leiocephalus personatus semilineatus—Cochran, 1941.

Leiocephalus semilineatus—Schwartz, 1967a, 1968.

Holotype.—MCZ 12748. Type locality: Thomazeau, Dépt de l'Ouest, Haiti.

Distribution.—Southcentral Hispaniola, west to Port-au-Prince, east to near Baní.

Characterization.—Small size (males to 53 mm, females to 48 mm SVL); nasal overlap of premaxillary spine complete; nasal-maxillary suture straight; nasal processes of frontal not exposed; frontal narrow; parietal table U-shaped in adults; supratemporal lateral; supratemporal process of squamosal indistinct; skull roof rugose; angular process of dentary well developed; transition to tricuspid crowns at Tooth 10 or 11 on

dentary; snout scale pattern Type III (2 rows of scales between internasals and anterior pair of frontals, with posterior row composed of 3, or a single pair of, enlarged scales); parietal scale pattern Type II (most lateral parietal scales subequal to or slightly larger than median pair, and single row [occasionally 2] of postparietals); 3 internasals, usually 2 in contact with rostral; 4 lorilabial scales anterior to enlarged subocular; cephalic scales essentially smooth; single, enlarged temporal scale usually present; lateral neck scales undifferentiated; lateral trunk scales not reduced; middorsal crest moderate, 49–63 dorsal crest scales occiput–vent; postanal escutcheons usually 4; tricarinate scales of first and second toe enlarged, fringe moderate; lateral neck folds moderate; nuchal fold moderately convex; lateral fold on trunk absent; facial band extending onto trunk; throat and venter immaculate.

Remarks.—Williams (1963) noted the association of this species with other xerophilous lizards, for example *Anolis whitemani*, in the open scrub of the Cul de Sac Plain and Valle de Neiba.

***Leiocephalus stictigaster* Schwartz, 1959b**

Holotropis microlophus Duméril and Bibron, 1837 (part).

Leiocephalus vittatus Boulenger, 1885 (part).

Leiocephalus cubeensis Barbour, 1916b (part).

Holotype.—AMNH 77864. Type locality: Beach on Cabo Corrientes, Pinar del Río Province, Cuba

Distribution.—Cuba island-wide, but scattered; Isla de la Juventud.

Characterization.—Moderately large size (males to 100 mm, females to 80 mm SVL); nasal overlap of premaxillary spine complete; nasal-maxillary suture curved; nasal processes of frontal not exposed; frontal narrow; parietal table U-shaped in adults; supratemporal lateral; supratemporal process of squamosal indistinct; skull roof rugose; angular process of dentary well developed; transition to tricuspid crowns at Tooth 10 or 11 on dentary; snout scale pattern Type II (3 rows between internasals and anterior frontals, with posterior row composed of 3 scales in con-

tact with anterior frontals); parietal scale pattern Type II (most lateral parietal scales subequal to or slightly larger than median pair, and single row [occasionally 2] of postparietals); 3 internasals, usually 2 in contact with rostral; 4 lorilabial scales anterior to enlarged subocular; cephalic scale ridges extending onto frontonasals; lateral neck scales undifferentiated; lateral trunk scales not reduced; middorsal crest moderate, 43–62 dorsal crest scales occiput–vent; postanal escutcheons usually 4; tricarinate scales of first and second toe enlarged, fringe moderate; lateral neck folds moderate; nuchal fold moderately convex; lateral fold on trunk absent; throat heavily patterned with chevrons or smudges; dorsum lineate.

Subspecies.—*stictigaster* Schwartz (1959b); *astictus* Schwartz (1959b); *celeustes* Schwartz and Garrido (1968a); *exotheotus* Schwartz (1959b); *gibarensis* Schwartz and Garrido (1968a); *lipomator* Schwartz and Garrido (1968a); *lucianus* Schwartz (1960a); *naranjoi* Schwartz and Garrido (1968a); *ophioplacodes* Schwartz (1964); *parasphex* Schwartz (1964); *septentrionalis* Garrido (1975); *sierrae* Schwartz (1959b).

Remarks.—Formerly confused with *Leiocephalus cubensis*, *L. stictigaster* was made specifically distinct by Schwartz (1959b), who subsequently designated trinomials for numerous populations.

***Leiocephalus vinculum* Cochran, 1928b**

Leiocephalus personatus vinculum—Cochran, 1941.

Leiocephalus vinculum—Schwartz, 1967a.

Holotype.—MCZ 25435. Type locality: Pointe à Raquettes, Ile de la Gonâve, Haiti.

Distribution.—Ile de la Gonâve, Haiti.

Characterization.—Moderate size (males to 77 mm, females to 73 mm SVL); nasal overlap of premaxillary spine complete; nasal-maxillary suture curved; nasal processes of frontal not exposed; frontal narrow; parietal table U-shaped in adults; supratemporal ventromedial; supratemporal process of squamosal indistinct; skull roof smooth; angular process of dentary well developed; transition to tricuspid crowns at Tooth 10 or 11 on dentary; snout scale pattern Type III (2 rows of scales between internasals and anterior pair of frontals, with posterior row composed of 3, or a single pair of, enlarged scales); parietal scale pattern Type III (most lateral parietals larger than median pair, postparietals few or absent); 3 internasals, usually 2 in contact with rostral; 4 lorilabial scales anterior to enlarged subocular; cephalic scales essentially smooth; lateral neck scales undifferentiated; lateral trunk scales not reduced; middorsal crest moderate; 51–60 middorsal crest scales occiput–vent; postanal escutcheons usually 4; tricarinate scales of first and second toe enlarged, fringe moderate; lateral neck folds simple; nuchal fold moderately convex; lateral fold on trunk absent; scapular or suprascapular pattern absent.

Remarks.—With the reallocation of *Leiocephalus altavelensis* (Noble and Hassler, 1933) to *L. barahonensis*, and the recognition of *L. endomachus* (Schwartz, 1967a) as a distinct species, *L. vinculum* is restricted to the monotypic population on Ile de la Gonâve.

SUMMARY

The iguanian lizard genus *Leiocephalus* is endemic to the West Indies, where 21 extant species are found on Cuba, the Bahamas, and Hispaniola. Two species that became extinct historically and six others known only by fossils document a previously greater range in the Antilles.

All of the species are terrestrial, largely xerophilous, and range from 55 mm to nearly 140 mm SVL; some fossil species may have reached 200 mm SVL. Living *Leiocephalus* resemble

other spiny, scansorial iguanians in general habitus and none is especially apomorphic. The monophyly of the genus is supported by at least 11 morphological synapomorphies. Species of *Leiocephalus* are members of a group that is otherwise exclusively South American—the Tropiduridae. My analysis of skeletal, integumentary, and soft-anatomical characters corroborates other recent studies that place them in the topology: [Liolaeminae [*Leiocephalus*, Tropidurinae]].

Relationships within *Leiocephalus* also were estimated with morphological criteria. Numerous potential character transformations were identified and a restricted suite that met the demands of discrete variation was chosen. Of the approximately 140 potential characters, 39 proved useful for estimating a phylogeny of the species. Based on these data, 12 equally parsimonious tree topologies were obtained. These trees differ in the placement of several terminal branches within three primary stems, which are as follow: (1) a clade composed of *L. carinatus*, *greenwayi*, and *punctatus*; (2) a complex here referred to as the *L. melanochlorus* group—*melanochlorus*, *psammodromus*, *inaguae*, *schreibersi*, and *macropus*; and (3) all remaining extant species except *herminieri* and *eremitus*. This large branch of 11 species configures as (((*loxogrammus* + *raviceps*) + (*lunatus* + *personatus*)) + (*cubensis* + *stictigaster*)) + (*rhutidira* + *semilineatus*) + (*vinculum*) + (*barahonensis*). There are equally parsimonious arrangements within this scheme for *lunatus* (as the sister species of *loxogrammus* + *raviceps*), and for *barahonensis* with respect to *rhutidira*, *semilineatus*, and *vinculum*. *Leiocephalus pratensis* displays no apparent affinity with any one species or group of species, and falls out as the sister species of this large, mostly Hispaniolan complex. My analysis reveals that *L. vinculum*, heretofore composed of three subspecific populations, is restricted to the nominate population on Ile de la Gonâve. *Leiocephalus vinculum altavelensis* is placed in the synonymy of *L. barahonensis*, whereas *L. v. endomychus* is recognized as specifically distinct and the sister species of *L. rhutidira*.

The problematic *Leiocephalus herminieri*, presumed to have come from Martinique but now extinct and known by only four specimens, possesses a peculiar combination of primitive and derived attributes that places it as the sister species of all other *Leiocephalus*. The best candidate for the least apomorphic extant species is *L. carinatus*. The status of *L. eremitus*, the extinct species of Navassa Island, remains ambiguous because only the holotype is known and most of its osteological characters could not be scored.

Possible relationships based on external characteristics are with *L. greenwayi*, *punctatus*, and *carinatus*, or with the *Leiocephalus melanochlorus* group.

None of the six named fossil *Leiocephalus* from the West Indies can be placed confidently on the tree of extant species because they are represented only by isolated and usually incomplete skeletal elements. Of the 13 cranial characters used in the primary analysis, none of these fossil taxa could be scored for more than eight of them. Inclusion of these six species into the primary data matrix effects tree topologies of the extant species mainly in the form of polytomies at terminal stems. Some of the fossil species, for example *L. anonymous* and *L. apertosulcus*, in fact may be more closely related to one another than to any extant species, based on an open Meckel's groove as a derived reversal. In any event, all of these West Indian fossil forms are clearly *Leiocephalus*, in contrast to others from Oligocene and Miocene deposits of North America. Most of these latter fossils are simply too incomplete for confident identification; their referral to *Leiocephalus* was based on possession of dentaries with a closed Meckel's groove and tricuspid tooth crowns posteriorly, and neither of these characters is compelling evidence for relationship. The most abundant material comes from the Valentine Formation of Nebraska and was described as *Leiocephalus nebraskensis*, but this form is neither *Leiocephalus* nor likely even a tropidurid.

Leiocephalus is relictual in the West Indies. Several of the fossil species demonstrate that the clade's former range included all of the major islands in the Greater Antilles and probably most banks of the Lesser Antilles, at least south to Martinique. New fossils from Anguilla and Guadeloupe are described herein and tentatively referred to *L. cuneus*, a fossil species known previously from Barbuda and Antigua. The causes of the extinction of these *Leiocephalus* may or may not be the same; where accurate chronologies are available, their demise is synchronous with European and African settlement of the Antilles.

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APPENDIX I.

Input data matrix for *Leiocephalus* character transformations (used in tree construction of Figs. 14–16, 18).

Node	Character																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																				
	1	2	3	4	5	6	7	8	9	0	1	1	1	1	1	1	1	1	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2

APPENDIX II.

Apomorphy list for tree in Figure 14; based on data matrix from Appendix I.

Stem	Character	Ancestral state	Derived state
<i>barahonensis</i>	23	0	1
	30	0	2
<i>carinatus</i>	25	1	0
<i>cubensis</i>	38	0	1
<i>eremitus</i>	21	0	1
<i>greenwayi</i>	11	0	1
	26	0	1
	28	0	1
	36	0	1
<i>herminieri</i>	6	0	1
	11	0	1
	18	3	1
	27	1	0
	39	0	1
<i>inaguae</i>	6	1	0
	10	1	0
	16	1	2
	21	1	0
	35	0	1
<i>loxogrammus</i>	1	1	0
	5	0	1
	6	0	1
	8	0	1
	11	1	0
<i>lunatus</i>	4	0	1
	12	1	0
	36	0	1
<i>macropus</i>	5	0	1
	20	1	2
	22	1	2
	36	0	1
	38	0	2
<i>melanochlorus</i>	2	1	0
	20	1	2
	22	1	2
	29	1	0
<i>personatus</i>	19	1	0

Appendix II Continued

Stem	Character	Ancestral state	Derived state
<i>pratensis</i>	38	0	1
	20	1	2
	27	1	2
	30	0	1
	38	0	2
<i>psammodromus</i>	9	0	1
<i>punctatus</i>	2	0	1
	7	0	1
	21	0	1
<i>raviceps</i>	22	1	2
	28	0	1
	34	0	1
<i>rhutidira</i>	5	0	1
	13	0	1
	29	1	2
<i>schreibersi</i>	7	1	0
	12	0	1
	14	0	1
	28	0	1
	35	0	1
<i>semilineatus</i>	9	0	1
	19	0	1
	38	0	2
<i>stictigaster</i>			
<i>vinculum</i>	11	1	0
	29	1	0
1	16	3	2
	22	1	2
2	14	0	1
	24	0	1
	38	0	2
3	27	1	0
4	15	0	1
	19	0	1
5	22	0	1

Appendix II Continued

Stem	Character	Ancestral state	Derived state
6	4	0	1
	23	0	1
7	9	1	0
	31	2	1
8	18	3	2
	33	1	2
9	7	1	0
	9	0	1
	11	0	1
	12	0	1
	22	1	0
10	16	1	3
	25	1	0
	31	0	2
	33	3	1
11	1	1	0
	3	0	1
	8	0	1
	22	1	0
	28	0	1
12	6	0	1
	10	0	1
	21	0	1
	37	0	1
	39	0	1
13	12	1	2
	32	0	1
14	2	0	1
	18	3	1
	26	0	1
	24	0	1
15	8	0	1
	30	1	0
16	16	1	2
	17	0	1
	31	0	1
17	30	0	1
	33	3	2

Appendix II Continued

Stem	Character	Ancestral state	Derived state
18	1	0	1
	5	1	0
	7	0	1
	22	0	1
	29	01	
19	20	0	1
20	16	0	1
	18	0	3
	30	0	3

APPENDIX III.

List of changes within transformation series for tree in Figure 14. U = unpolarized, UO = unordered transformation.

Character	Changed		Along stem	Consistency
	From	To		
1	0	1	18	0.333
	1	0	11	
	1	0	<i>loxogrammus</i>	
2	0	1	14	0.333
	0	1	<i>punctatus</i>	
	1	0	<i>melanochlorus</i>	
3	0	1	11	1.000
4	0	1	6	0.500
	0	1	<i>lunatus</i>	
5U	1	0	18	0.250
	0	1	<i>rhutidira</i>	
	0	1	<i>macropus</i>	
	0	1	<i>loxogrammus</i>	
6	0	1	12	
	0	1	<i>loxogrammus</i>	
	1	0	<i>inaguae</i>	

Appendix III Continued

Character	Changed		Along stem	Consistency
	From	To		
	0	1	<i>herminieri</i>	0.250
7	0	1	18	
	1	0	9	
	1	0	<i>schreibersi</i>	
	0	1	<i>punctatus</i>	0.250
8	0	1	11	
	0	1	15	
	0	1	<i>loxogrammus</i>	0.333
9	0	1	9	
	1	0	7	
	0	1	<i>semilineatus</i>	
	0	1	<i>psammodromus</i>	0.250
10	0	1	12	
	1	0	<i>inaguae</i>	0.500
11	0	1	9	
	1	0	<i>vinculum</i>	
	1	0	<i>loxogrammus</i>	
	0	1	<i>herminieri</i>	
	0	1	<i>greenwayi</i>	0.200
12	0	1	9	
	0	1	<i>schreibersi</i>	
	1	0	<i>lmatus</i>	0.333
13U	0	1	<i>rhutidira</i>	1.000
14	0	1	2	
	0	1	<i>schreibersi</i>	0.500
15	0	1	4	1.000
16UO	0	1	20	
	1	3	10	
	1	2	13	
	1	2	16	
	3	2	1	
	1	2	<i>inaguae</i>	0.500

Appendix III Continued

Character	Changed		Along stem	Consistency
	From	To		
17	0	1	16	1.000
18UO	0	3	20	0.750
	3	2	8	
	3	1	14	
	3	1	<i>herminieri</i>	
19	0	1	4	0.333
	0	1	<i>semilineatus</i>	
	1	0	<i>personatus</i>	
20	0	1	19	0.500
	1	2	<i>pratensis</i>	
	1	2	<i>melanochlorus</i>	
	1	2	<i>macropus</i>	
21	0	1	12	0.250
	0	1	<i>punctatus</i>	
	1	0	<i>inaguae</i>	
	0	1	<i>eremitus</i>	
22	0	1	18	0.250
	1	0	9	
	0	1	5	
	1	0	11	
	1	2	1	
	1	2	<i>raviceps</i>	
	1	2	<i>melanochlorus</i>	
	1	2	<i>macropus</i>	
23	0	1	6	0.500
	0	1	<i>barahonensis</i>	
24	0	1	2	1.000
25U	1	0	10	0.500
	1	0	<i>carinatus</i>	
26U	0	1	14	0.500
	0	1	<i>greenwayi</i>	
27U,UO	1	0	3	

Appendix III Continued

Character	Changed		Along stem	Consistency
	From	To		
28U	1	2	<i>pratensis</i>	0.667
	1	0	<i>herminieri</i>	
	0	1	11	0.250
	0	1	<i>schreibersi</i>	
	0	1	<i>raviceps</i>	
	0	1	<i>greenwayi</i>	
29	0	1	18	0.500
	1	0	<i>vinculum</i>	
	1	2	<i>rhutidira</i>	
	1	0	<i>melanochlornis</i>	
30UO	0	1	17	0.500
	1	0	15	
	0	1	<i>pratensis</i>	
	0	2	<i>barahonensis</i>	
31UO	0	2	10	0.667
	2	1	7	
	0	1	16	
32	0	1	13	1.000
33UO	0	3	20	0.750
	3	1	10	
	1	2	8	
	3	2	17	
34	0	1	14	0.500
	0	1	<i>raviceps</i>	
35	0	1	<i>schreibersi</i>	0.500
	0	1	<i>inaguae</i>	
36	0	1	<i>macropus</i>	0.333
	0	1	<i>lunatus</i>	
	0	1	<i>greenwayi</i>	
37	0	1	12	1.000
38U,UO	0	2	2	

Appendix III Continued

Character	Changed		Along stem	Consistency
	From	To		
	0	2	<i>semilineatus</i>	
	0	2	<i>pratensis</i>	
	0	1	<i>personatus</i>	
	0	2	<i>macropus</i>	
	0	1	<i>cubensis</i>	0.333
39	0	1	12	
	0	1	<i>herminieri</i>	0.500

APPENDIX IV.

Specimens examined. Abbreviations are given in the acknowledgements. S = skeleton or skeletal series.

Leiocephalus apertosulcus: UF 10088–10101, 55802. *L. anonymous*: USNM(VP) 340183–340192.

L. barahonensis: SDSNH 64667(S); USNM 80326, 80379, 224972, 224973. *L. b. barahonensis*: SDSNH 64570–64574(S), 64575–64577, 64578(S), 64579(S), 64580–64583. *L. b. aureus*: MCZ 68612, 68613; REE 1809(S). *L. b. beatanus*: ASFS V2726, V2729, V17203; REE 1821; USNM 83875, 84283, 85059(S). *L. b. oxygaster*: SDSNH 64584, 64585. *L. b. oxygaster* × *aureus*: SDSNH 64586, 64587.

L. cuneus: UF 8226–8233, 8263–8271, 8444, 8468–8470; USNM(VP) 340157–340164, 340196.

L. carinatus: ASFS V22390, V22393, V22394; MCZ 141246(S); UMMZ 149103(S); USNM 81709(S), 220646. *L. c. aquarius*: SDSNH 65958, 65966(S), 65983(S), 65997. *L. c. armouri*: ASFS V8954, V8966, V36187; MCZ 6966(S), 6966b(S); USNM 158895. *L. c. coryi*: ASFS X4746, X4747, X4752. *L. c. granti*: MCZ 45127–45130; REE 1469(S). *L. c. helenae*: MCZ 38112, 38115. *L. c. microcyon*: MCZ 11187(S), 11188(S). *L. c. varius*: ASFS V11682, V11684, 16144; USNM 81750–81752, 217299(S). *L. c. virescens*: MCZ 141247(S); REE 1505.

L. cubensis: CAS 39304(S), 39305–39308;

CAS–SU 9247–9254, 14617–14623; MCZ 150341, 150342; SDSNH 65833(S), 66335(S); USNM 27999, 138643.

L. eremitus: USNM 12016.

L. etheridgei: USNM(VP) 259190–259202.

L. greenwayi: MCZ 36711, 36716(S), 162032, 162033; REE 1814(S); UMMZ 94051, 114518, 149108(S); USNM 120766, 149108(S).

L. herminieri: BM(NH) 52.12.3.10(S); MNHN 6829.

L. inaguae: ASFS 10337; LSUMZ 30265–30270, 30272, 30275; MCZ 154263(S); UMMZ 149133(S); USNM 81277, 89375.

L. jamaicensis: AMNH 2311–2315; UF 8489–8493, 8496, 8505, 8511–8513.

L. loxogrammus loxogrammus: MCZ 38131(S), 38135(S); SDSNH 66342(S), 66343–66345, 66346(S), 66347(S), 66348–66352, 66353(S), 66354; UMMZ 149134(S); USNM 14569. *L. l. parnelli*: KU 192293; USNM 220526, 220529, 220537, 220576–220596(S).

L. lunatus arenicolor: MCZ 75079–75082; SDSNH 64588; USNM 40919, 40920. *L. l. arenicolor* × *lewisi*: SDSNH 64610–64612, 64613–64617(S), 64618–64620, 64621(S). *L. l. lewisi*: SDSNH 64589–64599, 64600–64602(S), 64604–64608, 64609(S); USNM RD145, RD147. *L. l. louisie*: USNM 40210, 40211. *L. l. melaenacelis*: USNM 40912, 40914, 40916. *L. l. thomasi*: REE 1815(S).

- L. macropus*:** MCZ 11208(S); REE 1819(S). *L. m. macropus*: SDSNH 65959, 65960, 65965(S), 65989(S), 66002, 66004(S), 66005(S), 66012; USNM 25819, 220653(S), 220721. *L. m. asbolomus*: USNM 220654–220656(S), 220722, 220723. *L. m. immaculatus*: USNM 220647–220652(S).
- L. melanochloris*:** MCZ 3598, 37533(S), 59545(S); SDSNH (4 spec. uncat.); USNM 80852, 80858(S), 80859, 80860. *L. m. hypsistus*: MCZ 59545.
- L. nebraskensis*:** USNM 47025, 47075, 47088, 47134, 47144, 47146, 47148, 51812, 51813, 51815, 51818, 51819, 56049, 56085, 56092, 56093.
- L. partitus*:** KUPV 11473; USNM(VP) 259203.
- L. personatus*:** MCZ 3615; REE 1811; SDSNH 10781–10783. *L. p. budeni*: KU 93316–93321. *L. p. mentalis*: SDSNH 64630, 64631, 64644(S). *L. p. scalaris*: MCZ 58038(S), 58044(S), 58051(S); REE 1803; USNM 224975–224978, 225044(S), 225045(S). *L. p. socoensis*: SDSNH 64622(S), 64623–64626, 64627(S), 64628, 64629. *L. p. tarachodes*: ASFS V16137, V16139, V16140. *L. p. trujilloensis*: ASFS X9249, V14577, V14578.
- L. pratensis*:** MCZ 61229, 56044(S); USNM 69189, 74121, 74124, 74127. *L. p. chimaris*: ASFS V9841(S), V9843, V9846.
- L. psammodromus*:** LSUMZ 30364–30368, 30373–30379, 30385; MCZ 11948; REE 1813(S); UMMZ 149109(S); USNM 81385. *L. p. aphretor*: MCZ 54191, 54192. *L. p. mounax*: MCZ 54170, 86141, 86143(S), 86146.
- L. punctatus*:** ASFS V10999, V27421, V27423(S), V27424, V27515, V27529; MCZ 38083(S), 38087(S); UMMZ 81560, 149110(S).
- L. raviceps*:** MCZ 13376(S); UMMZ 149111(S); USNM 4162, 220657–220665, 220724, 220729. *L. r. raviceps*: SDSNH 65928, 65936, 65963, 65964(S), 65985, 65986(S), 65987(S), 65993(S).
- L. rhutidira*:** ASFS V46324, V46742, V46748(S), V46750.
- L. schreibersi*:** REE 1815; SDSNH 64665(S), 64666(S), 64668–64670(S), 64671–64678; USNM 40021, 40022. *L. s. schreibersi*: MCZ 39592(S), 59591(S), 64908, 64911, 65791(S); USNM 40021, 40022. *L. s. nesomorus*: MCZ 37556, 37564.
- L. semilineatus*:** MCZ 58069, 58073; SDSNH 64632(S), 64633, 64634(S), 64635(S), 64636, 64637(S), 64638, 64639(S), 64640(S), 64641, 64642, 64643(S); USNM 40077, 40081, 225046–225048(S), 259510(S).
- L. stictigaster***: *L. stictigaster*: AMNH 77864; MCZ 118706, 118870. *L. s. celestes*: MCZ 92021, 92022. *L. s. exotheotus*: MCZ 11114, 11115. *L. s. gibarensis*: ASFS V11763, V11764(S), V11765. *L. s. luciamus*: MCZ 59228(S); REE 1810. *L. s. naranjoi*: USNM 140466, 140467.
- L. vinculum*:** MCZ 25435, 25437; REE 1812. *L. v. vinculum*: ASFS X2495, V26619(S). *L. v. altavelensis*: ASFS V26908, V26909. *L. v. endomychus*: ASFS V43786, V43788, V43795.
- Liolaemus*:** *L. anomalus*: MCZ 19053, 19054; REE 2283(S). *L. austromendocinus*: MCZ 19110, 19112; REE 2343(S). *L. bibioni*: MCZ 19313, 19314; REE 2406(S). *L. boulengeri*: REE 2458(S). *L. darwini*: MCZ 19170, 19171; REE 2495(S). *L. eleodori*: REE 2376(S). *L. elongatus*: MCZ 19233, 19234; REE 2366(S). *L. e. petrophilus*: REE 2428(S). *L. fitzingeri cuyanus*: REE 2316(S). *L. k. kingi*: REE 2481(S). *L. kriegi*: REE 2417(S), 2418(S). *L. lineomaculatus*: REE 2465(S). *L. multiformis*: REE 1826(S), 1827(S). *L. pictus*: REE 1897(S), 1874(S). *L. rothi*: REE 2398(S), 2400(S). *L. ruibali*: REE 2301(S).
- Ophryoessoides*:** *O. aculeatus*: KU 121092, 121093(S), 121094; UMMZ 149102. *O. arenarius*: WP 544(S), 577(S). *O. caducus*: KU 136354, 136355; REE 2285(S). *O. guentheri*: WP 541(S), 549–551(S). *O. iridescens*: KU 121139–121141, 142683, 142695(S), 164170. *O. i. cajamareae*: REE 1820(S); USNM 200912(S), 222585(S). *O. trachecephalus*: REE 234(S).
- Phymaturus*:** *P. palluma*: REE 2323(S), 2325(S), 2326(S). *P. patagonicus patagonicus*: REE 2472(S). *P. p. payunia*: REE 2336(S). *P. p. somuncurensis*: MCZ 19284, 19285; REE 2436(S).
- Plica*:** *P. plica*: KU 167499(S); REE 2167(S). *P. umbra*: KU 125968(S); USNM 204266(S).
- Procotretus*:** *P. pectinatus*: KT 187794(S), 187798(S).
- Stenocercus*:** *S. apurimacus*: KU 134270, 134278(S), 134283, 134284(S), 134288. *S. boettgeri*: KU 134014(S). *S. chrysopygus*: KU 133895(S). *S. crassicaudatus*: REE 2284(S), 2286(S). *S. cupreus*: KU 133974(S). *S. empetrus*: KU 134404(S). *S. festae*: KU 134595(S), 141150, 141151. *S. formosus*: KU 134110(S). *S. guentheri*: KU 147347, 169857, 192678, 192679; USNM 222584(S). *S. humeralis*: KU 134004(S). *S.*

- nigromaculatus*: KU 134092(S). *S. praeornatus*: KU 97856(S); REE 2470. *T. stolzmani*: KU 134701, 134706, 134708, 134726. *T. theresoides*: KU 162012(S), 162018(S). *T. thoracicus*: KU 163724(S). *T. torquatus*: REE 324(S); USNM 222582(S).
- Strobilurus***: *S. torquatus*: MCZ 133243(S).
- Tapinurus***: *T. semitaeniatus*: REE 1801(S).
- Tropidurus***: *T. atacamensis*: KU 161983(S). *T. barringtonensis*: SDSNH 30929(S). *T. etheridgei*: KU 186113(S). *T. hispidus*: KU 167508(S). *T. kopckeorum*: KU 163604, 163606, 163607. *T. occipitalis*: WP 547, 556. *T. peruvianus*: KU 134674(S), 164055(S), 164056(S). *T. spinulosus*: KU 97856(S); REE 2470. *T. stolzmani*: KU 134701, 134706, 134708, 134726. *T. theresoides*: KU 162012(S), 162018(S). *T. thoracicus*: KU 163724(S). *T. torquatus*: REE 324(S); USNM 222582(S).
- Uranoscodon***: *U. superciliaris*: KU 135269(S). *U. superciliosa*: MAN 44(S); REE 2508, 2511(S).
- Urocentron***: *U. flaviceps*: REE 924.
- Vilcunia***: *V. periglacialis*: MCZ 122010, 162007, 162008(S), 162009. *V. sylvanae*: MCZ 156906(S).